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Fishery Bulletin

Scientific Editor
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National Marine Mammal Laboratory
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE
Seattle, Washington 98115-0070

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Scientific Publications Office
7600 Sand Point Way NE, BIN C15700
Seattle, Washington 98115-0070

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Abstract.– Ages were estimated for sheepshead *Archosargus probatocephalus* (Pisces:Sparidae) from Louisiana waters using transverse sections of sagittae (otoliths). Opaque annuli were validated to have formed in sagittae once per year during April and May in 1987 and 1988. Age range was 1–20 years for fish measuring 22–56 cm fork length and weighing 0.4–3.6 kg. Von Bertalanffy growth models were different for males and females; females exhibited a faster growth rate and achieved larger maximum sizes. There was great variability in age at a given length or weight, which precludes the use of morphometrics as age indices. Otolith weight provided a more precise estimate of age than fish length or weight. The consideration of fish length or weight in addition to otolith weight significantly improved the predictive capability of multiple regression models.

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Age and Growth-Rate Estimation of Sheepshead *Archosargus probatocephalus* in Louisiana Waters Using Otoliths

Daniel W. Beckman
A. Louise Stanley
Jeffrey H. Render
Charles A. Wilson

Coastal Fisheries Institute, Center for Wetland Resources
Louisiana State University, Baton Rouge, Louisiana 70803-7503

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The sheepshead *Archosargus probatocephalus* is an estuarine/marine sparid common in coastal waters of the northern Gulf of Mexico. This species supports significant commercial and recreational fisheries off Louisiana. Louisiana commercial landings of sheepshead have increased substantially in recent years, from 59 to 1111 metric tons between 1981 and 1989 (NMFS 1982, 1990), resulting in concern for the species and consideration of development of a management plan. However, little has been reported on sheepshead biology and population dynamics. Of particular concern is the lack of information on age and growth. The only information reported are average growth rates for juveniles in North Carolina (Hildebrand and Cable 1938) and Florida (Springer and Woodburn 1960). The development of valid management plans based on the current available information would be difficult.

Otolith analyses have been proven valid for age estimation of several fish species occurring in the temperate waters of the northern Gulf of Mexico (Johnson et al. 1983, Barger 1985, Beckman et al. 1989, Beckman et al. 1990a). Sectioning of otoliths is often required in order to accurately enumerate annuli for age estimation, especially for long-lived species with large robust otoliths. Sample preparation and ageing are often labor intensive. As an alternative, Boehlert (1985) suggested that otolith size may provide objective, repeatable age estimates and save time and cost in sample processing. Several studies have documented otolith size as greater for older fish than for younger fish of the same size (Templeman and Squires 1956, Wilson and Dean 1983, Boehlert 1985, Reznick et al. 1989, Secor and Dean 1989), and suggested that otolith weight be used to estimate age.

The purposes of this study were to validate age estimates of sheepshead in Louisiana waters using otolith (sagitta) transverse sections, to derive fish growth models, and to determine the potential of using otolith weight for age estimation of this species.

Methods

We sampled sheepshead ($n = 784$) from February 1987 to August 1988. Samples were taken by commercial gillnet (15–18 cm [6–7 inch] stretch mesh) ($n = 461$), trawl ($n = 163$), and haul seine ($n = 43$); recreational hook-and-line ($n = 38$) and spearfishing ($n = 27$); and unknown gear types ($n = 52$). Gillnet and haul seine samples were predominantly from inshore waters in the Mississippi Delta–Lake

Table 1

Summary of age and growth analyses of sparids. K and L_∞ are parameters from von Bertalanffy growth models. Age and length are the maximums reported by the source. Lengths marked (*) are total lengths, others are fork lengths. M and F refer to parameters for males and females, when reported.

Species	Source	Location		K	L_∞	Age (max.)	Length (max.)
Archosargus probatocephalus	This study	N. Gulf of Mexico	(M)	0.42	419	20	500
			(F)	0.37	446	20	500
Stenotomus caprinus	Geoghegan and Chittenden (1982)	N. Gulf of Mexico		—	—	3	193
Calamus leucosteus	Waltz et al. (1982)	U.S. Atlantic		0.17	331	12	410
Pagrus pagrus	Manooch and Huntsman (1977)	U.S. Atlantic		0.10	763	15	*690
Stenotomus chrysops	Finkelstein (1969)	U.S. Atlantic	(M)	0.27	343	15	370
			(F)	0.23	374		
Cheimerius nufar	Coetzee and Baird (1981)	South Africa		0.07	954	22	*705
Cymatoceps nasutus	Buxton and Clarke (1989)	South Africa		0.05	1090	45	1099
Pachymetopon aeneum	Buxton and Clarke (1986)	South Africa		0.13	467	12	400
Pachymetopon blochii	Pulfrich and Griffiths (1988)	South Africa		0.16	411	12	350
Pterogymnus laniarius	Hecht and Baird (1977)	South Africa		0.19	481	11	*422
Pagellus bellottii	Koranteng and Pitcher (1987)	Ghana	(M)	0.38	257	6	250
			(F)	0.23	286		
Pagrus major	Sakamoto (1984)	Japan		0.21	670	10	590
Chrysophrys auratus	Horn (1986)	New Zealand		—	—	60	650

drum *Pogonias cromis* (January–April; Beckman et al. 1990a), and Atlantic croaker *Micropogonias undulatus* (February–April; Barger 1985) in the northern Gulf of Mexico. It is likely that annulus formation in sagittae of these species is in response to environmental factors and is not related to reproductive seasonality, since all three species exhibit different spawning seasons: red drum, August–October (Wilson et al. 1989); black drum, December–April (Beckman et al. 1990b); Atlantic croaker, September–March (White and Chittenden 1987).

Sheepshead are relatively long-lived, with a maximum life span of at least 20 years based on our estimates. Greater ages are likely since the Louisiana gamefish record is 9.6 kg (Louisiana Outdoor Writers Assoc. 1987), and the maximum sized fish in this study was 3.9 kg. The maximum age we observed for sheepshead is greater than reported for other Gulf/U.S. Atlantic sparids (Table 1). However, great longevity is apparently not unusual for this family, as greater maximum ages have been reported for sparids elsewhere (Table 1).

Length–weight regressions for males and females were not significantly different ($P = 0.991$ for intercepts, $P = 0.647$ for slopes). However, since the exponents are used in growth models, regressions are presented for both sexes. Regressions were,

for males:

$$\text{Weight} = 4.48 \times 10^{-5}\ \text{FL}^{2.88} \quad r^2 = 0.943$$

for females:

$$\text{Weight} = 5.30 \times 10^{-5}\ \text{FL}^{2.85} \quad r^2 = 0.926$$

sexes combined:

$$\text{Weight} = 5.46 \times 10^{-5}\ \text{FL}^{2.86} \quad r^2 = 0.923.$$

The separation of sexes in growth models resulted in a significantly better fit by length and weight when compared with models in which sexes were combined ($P<0.001$). Therefore, separate von Bertalanffy growth curves for males and females were used to model growth in length (Fig. 3) and weight (Fig. 4). Residuals appeared normally distributed about the regression lines. Growth models fit were, by length,

males:

$$L_t = 419(1 - e^{-0.417(t+0.901)}) \quad r^2 = 0.589$$

females:

$$L_t = 447(1 - e^{-0.367(t+1.025)}) \quad r^2 = 0.532,$$

and by weight,

males:

$$W_t = 1900(1 - e^{-0.280(t+2.657)})^{2.88} \quad r^2 = 0.549$$

females:

$$W_t = 2557(1 - e^{-0.219(t+3.061)})^{2.85} \quad r^2 = 0.474,$$

The growth curves suggest rapid growth for sheepshead to an age of 6–8 years, after which an asymptote is approached. The values of K, the von Bertalanffy growth coefficient, for sheepshead are relatively high when compared with other sparids (Table 1) and to non-sparid perciform fish of similar size (see Pauly 1980). This indicates that sheepshead exhibit relatively rapid growth to an asymptotic size. This could be a result of living in the highly productive waters adjacent to the Mississippi Delta.

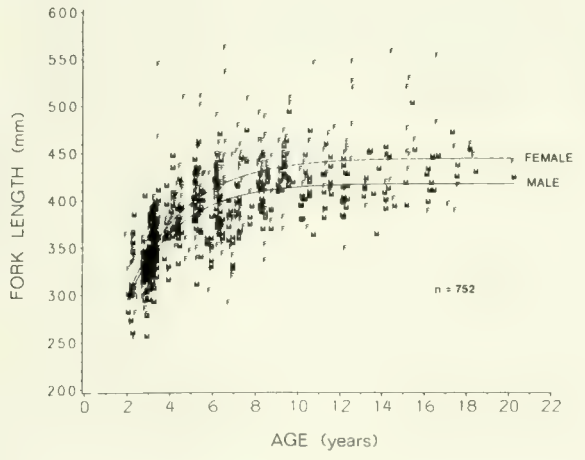

Figure 3
Von Bertalanffy growth models by length for male and female sheepshead. M = male; F = female.

Figure 4
Von Bertalanffy growth models by weight for male and female sheepshead. M = male; F = female.

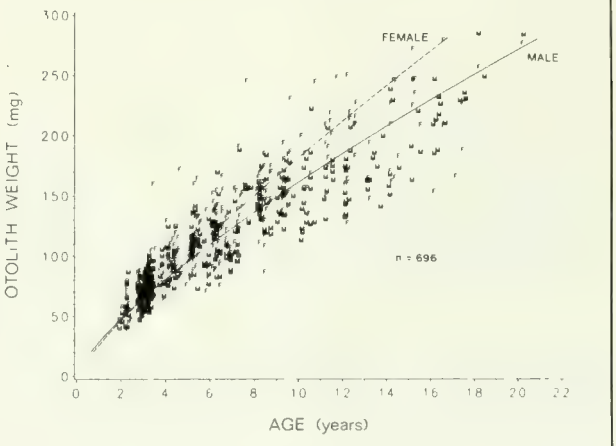

Figure 5
Log-linear growth models by otolith weight for male and female sheepshead. M = male; F = female.

Due to the large variability in age at a given body size, size does not accurately estimate age for sheepshead, especially beyond 2–3 years of age. For example, a given sheepshead greater than 400 mm or 1.5 kg could be of any age from 3 to 20 years.

Otoliths ranged in weight from 28.3 mg (for a 229-mm, 312-g, 2-year-old fish) to 323.5 mg (for a 450-mm, 2410-g, 18-year-old fish). Age-otolith weight (OW) regressions (Fig. 5) were significantly different for males and females ($P<0.0001$ for slopes, $P = 0.0006$ for intercepts); therefore multiple-regression models were fit separately by sex. Dependent variables included in multiple regression models at the 0.10 level of significance were otolith weight and total weight for males, and otolith weight and fork length for females. The addition of any other variables did not significantly improve the fit of the models. The model statistics are presented in Table 2.

Since otolith weight accounted for more of the variability in age (83–85% vs. <60% for fish length or weight), it was the best estimator of age of all morphometric variables considered. However, there was still considerable variability in otolith weight within each age class. Although some of the remaining variability (1–2%) was accounted for by considering fish length or weight in addition to otolith weight, the unexplained variability was great enough that these models could not be used for precise estimation of sheepshead age, such as is needed to determine population year-class structure. However, they could be used to approximate age distribution patterns in the population. In order to obtain precise age estimates of individual fish, otolith annulus counts are necessary.

The linear relationship between otolith weight and age indicates that otolith growth is continuous for sheepshead, whereas fish size (length and weight) asymptotes at intermediate ages and, therefore, is not continuous. This suggests that fast-growing (younger) sheepshead have lighter otoliths than equal-sized slow-growing (older) sheepshead, i.e., otolith growth continues with age, independent of fish growth. This may be a general characteristic of fish growth, as similar observations have been made for other fish species (Templeman and Squires 1956, Beamish 1979, Wilson

Table 2

Regression coefficients and statistics on multiple-regression models of age for sheepshead. Models were fit in a stepwise manner using independent variables of otolith weight, fish standard length, fish total weight, condition factor, and associated interaction terms. Variables were log-transformed for analyses.

Variable	Coefficient	SE	P	Partial r^2
Males (n = 330)				
(1-variable model)				
Intercept = −4.420				
Otolith weight	1.321	0.0305	<0.0001	0.850
(2-variable model)				
Intercept = −3.207				
Otolith weight	1.569	0.0594	<0.0001	0.850
Total weight	−0.331	0.0686	<0.0001	0.010
Females (n = 366)				
(1-variable model)				
Intercept = −3.824				
Otolith weight	1.176	0.0276	<0.0001	0.832
(2-variable model)				
Intercept = 1.258				
Otolith weight	1.484	0.0502	<0.0001	0.832
Fork length	−1.094	0.1531	<0.0001	0.021

and Dean 1983, Radtke et al. 1985, Reznick et al. 1989, Secor et al. 1989). Since fish length or weight accounts for significant variability in age after considering otolith weight, large fish have larger otoliths than equal-aged small fish, i.e., otolith growth is affected by fish growth. These observations support the proposition by Secor and Dean (1989) that not only do otoliths grow in a continuous manner, independent of somatic growth, but also that otolith growth is coupled in some manner to somatic growth.

These growth patterns should be considered when using otoliths for back-calculation of fish size at age. Since continued otolith growth uncoupled from somatic growth would result in slower-growing fish having larger otoliths at a given fish size, the fish-otolith size relationship would be different for fast-growing and slow-growing fish. This bias would be more pronounced at older ages, since otolith growth could continue even if somatic growth has stopped.

Due to gear selectivity and sorting of some samples by fishermen, the age distribution of our samples was not considered to be representative of the Louisiana sheepshead population. Future research should include fishery-independent sampling to accurately characterize the age structure of the sheepshead population, determine variability in recruitment, estimate mortality rates, and identify sources of variability in growth. Additional samples of older fish are required to complete validation of age estimates for the oldest individuals.

Acknowledgments

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1989 Age, growth, and the reproductive biology of schooling red drum from the northern Gulf of Mexico. 1988–1989 final report to Louisiana Department of Wildlife and Fisheries and U.S. Department of Commerce, Marine Fisheries Initiative (MARFIN) Program. Louisiana State Univ., Coastal Fish. Inst., Baton Rouge, 18 p.

Abstract. – Batch fecundity, weight-specific fecundity (number of eggs per gram somatic weight), size of ripe ovarian eggs, and the somatic and gonadal conditions of adult female queenfish *Seriphus politus* were estimated for five spawning seasons during an 8-year (1979–86) period. The effects of female somatic weight were evaluated in analyses of covariance comparing batch fecundity, egg size, and gonadal condition among years.

Batch fecundity was positively (and allometrically) related to female somatic weight. Fecundities were remarkably similar during four of the five years evaluated. After adjustment for annual differences in female size, fecundities were still significantly lower (by about one-fifth) during 1984, a major El Niño year, compared with the preceding (1979–80) or following (1985–86) pairs of years. Gonadal condition also was uniquely low in 1984. The 1984 declines in fecundity and gonadal condition co-occurred with low somatic condition during 1984, particularly for larger females. Mean size (diameter, dry weight) of eggs was indistinguishable among years. There was a positive relation between egg size and female body size, and a general decline in egg size as the spawning season advanced for females of all sizes.

Likely links between declines in fecundity, gonadal and somatic condition, and the crash in planktonic production during the 1982–84 El Niño are discussed.

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Annual Variations in Fecundity, Egg Size, and the Gonadal and Somatic Conditions of Queenfish *Seriphus politus* (Sciaenidae)

Edward E. DeMartini

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole Street, Honolulu, Hawaii 96822-2396

Few data exist on annual variations in reproductive traits (fecundity, egg size, gonadal allocation) of marine fishes. At a minimum, however, such data are necessary if fisheries ecologists are to begin to understand the many processes, including the vagaries of planktonic transport, that influence the large annual and longer-term temporal fluctuations in the recruitment and subsequent year-class abundance of marine fish stocks (Sinclair 1988, Bailey and Almatar 1989). The influences of egg size and quality on the early growth and survivorship of most species are poorly understood (Ware 1975).

The queenfish *Seriphus politus* is a small croaker abundant in the inner-shelf waters off southern California. It has planktonic egg and larval stages prior to the recruitment of juveniles to epibenthic habitat. Individual females are indeterminate serial spawners that produce as many as 20 batches of eggs during a protracted (6-month) spawning season (DeMartini and Fountain 1981). Juvenile and small adult, including male, queenfish feed on zooplankton (copepods and mysids), and large adults, females in particular, specialize on juveniles of the northern anchovy *Engraulis mordax* (DeMartini et al. 1985).

In this paper, I present data on batch and relative (weight-specific) fecundities, egg size, and the gonadal and somatic conditions of adult female queenfish collected during five spawning seasons spanning an 8-year period from 1979 to 1986. Fecundity, egg size, and condition indices are compared among years and related to concurrent variations in female body size. Because data are available prior to, during, and immediately following a major El Niño event, I interpret my observations in terms of known interannual variations in planktonic production and potential food limitation.

Methods

Sample collection

Queenfish were collected during the March–August reproductive seasons (DeMartini and Fountain 1981) of 1979, 1980, 1984, 1985, and 1986. Nighttime (2000–0200 hours), biweekly to fortnightly collections with a lampara seine, made at 5–16 m bottom depths at three longshore locations in San Onofre–Oceanside waters (DeMartini et al. 1985), were used to index the abundance and to describe the size (length, weight) composition of the nearshore queenfish stock. Sample fish for gonad analyses were provided by daytime lampara seining, otter trawling, and gillnetting at <16-m depths in the same area, and by screenwell samplings of the San Onofre Nuclear Generating Station,

near San Clemente, California. Nighttime samples were used to characterize abundance and size composition, because net avoidance is less at night (Allen and DeMartini 1983). Fish analyzed for reproductive variables and condition were collected during daylight hours, because oocytes destined for imminent spawning are macroscopically recognizable within ovaries only as they hydrate during the half-day preceding dusk spawning (DeMartini and Fountain 1981).

Table 1

Size composition and catch-per-net-haul (CPUE) of adult female queenfish *Seriphus politus* collected during the March–August periods of 1979–86, off northern San Diego County, California. All fish were captured by lampara seines of consistent dimensions, mesh sizes, and method of deployment, during the night at 5–16 m bottom depths (DeMartini and Fountain 1981, DeMartini et al. 1985).

	SL (mm)		Mean somatic	Mean	Number	
Year	$\bar{x}$	% >165 mm	wt (g)	CPUE	Fish	Net hauls
1979	141	19	45	22	872	40
1980	134	16	40	22	995	45
1984	132	2	35	15	294	20
1985	134	6	38	20	624	32
1986	138	7	40	24	948	40

Processing of samples

Queenfish were refrigerated until processed within one day of collection. Sex and maturity were determined from macroscopic characteristics of gonads (DeMartini and Fountain 1981). Adult females were measured (standard length, SL, in mm), and their gonadectomized, wet body weights (as a proxy for somatic weight) were determined to 0.1 g.

Ovary and egg analyses

Both ovaries were removed (fresh) from adult females, weighed damp to 0.01 g, and, for fish in ripe(ning) condition, the presence of hydrated-state oocytes noted based on macroscopic criteria ("Stage 3" ovaries: DeMartini and Fountain 1981).

Hydrated-state ovaries were fixed and preserved in modified Gilson's Fluid (Bagenal and Braum 1971) for about three months, after which declines in oocyte diameters and dry weights should have stabilized (Wittames and Walker 1987). These specimens are hereafter referred to as "Gilson's-fixed." Batch fecundity was then determined for a maximum of 10 females per month and year of collection. Fecundity was estimated by gravimetric method (Bagenal and Braum 1971, DeMartini and Fountain 1981). Counts from each section were standardized to the total weight of both ovaries and then averaged (Hunter et al. 1985).

In a subsample of the Gilson's-fixed ovaries, I estimated the median diameter (random axis) of hydrated-state eggs: 10 randomly chosen oocytes per ovary pair were measured within ±25 μm (±1 "eyepiece unit" or "EU") using a compound microscope with ocular micrometer at 40× magnification. I examined a maximum of 10 females per month and year.

A linear dimension such as diameter might not accurately represent egg volume or mass because of variations in chemical composition or density (Blaxter and Hempel 1963). Therefore, I compared the diameter and dry weight of oocytes from Gilson's-fixed ovaries. For 46 females with hydrated-state ovaries present in March–August 1984 collections, I determined the mean dry weight of hydrated oocytes for one member of each ovary pair. I determined the mean diameter of hydrated oocytes for the other member of the ovary pair. Oocyte diameters were measured as described above. I determined mean oocyte dry weight by drying lots of 100 eggs to constant weight (1–2 days) in a vacuum jar over anhydrous calcium chloride. Eggs were dried at room temperature to avoid weight loss of volatiles (Hay 1984, Hislop and Bell 1987), and an aggregate weight determined to the nearest mg on an analytical balance.

Calculation of condition indices

The relative allocation of energy to gonadal tissue was indexed by the RGI of Erickson et al. (1985), as RGI = $(G/W^b) \times 100$, where G = wet weight of ovaries in g, W = wet somatic weight in g, and b = the exponent of the power equation, $G = aW^b$. The relative gonadal index (RGI) is equivalent to $100 \times a$, where a is defined by the linearized (log-transformed) equation, $\ln G = \ln a + b \ln W$ (Erickson et al. 1985). It was necessary to adjust the gonadal index for somatic weight because the slope of the logarithmic gonad-to-somatic weight equation was significantly greater than one (i.e., the relation was allometric).

I first attempted to index somatic robustness as relative somatic condition, $K_n = CW/SL^b$ (Le Cren 1951), where W = wet somatic weight in g, SL = standard length in mm, C = a constant (10^5), and b = the exponent of the regression, $W = aSL^b$. However, the exponent, evaluated as the slope of the log-transformed weight-to-length equation $\ln W = \ln a + b \ln SL$, differed among years, thereby invalidating the use of such an index in analysis of covariance (Erickson et al. 1985,

Cone 1989). I therefore limited my evaluation of robustness to comparisons of estimates of ordinary least-squares regression parameters (Cone 1989).

The relationship between wet and dry body weights might change throughout the spawning season (Love 1970). Therefore, I evaluated seasonal changes in dry somatic weight using 57 females collected at the start of (April–May, $n = 32$) and immediately following (August–September, $n = 25$) the 1985 spawning season. After ovarectomy, fish were frozen in air-tight "zip-lock" bags. Fish were then thawed, and each entire fish was macerated and individually oven-dried to a constant weight at 120°C for 24–32 hours.

Statistical analyses

I used nonparametric analysis of variance (Kruskal-Wallis One-way ANOVA) to compare the body lengths and somatic weights of females among years. Year was evaluated as a fixed-effect class variable, because I was interested in evaluating potential differences among a preestablished series of years. Analysis of covariance (ANCOVA) was used whenever possible to evaluate the effects of sampling year on batch fecundity, and on relative gonadal condition, after adjustment for year differences in somatic weight. A two-way Model I ANCOVA was used to evaluate subseasonal (approximately bimonthly) influences of egg diameter among years for females of differing body lengths. Dry egg weight was related to egg diameter by parametric regression. Dry somatic weight was regressed on wet weight for sample fish collected at the beginning and at the end of the 1985 spawning season; regressions were then compared using ANCOVA with body length as the covariate. Computations were made using the GLM, REGRESS and TTEST software procedures of the Professional Database Analysis System (PRODAS; Conceptual Software Inc. 1986).

Table 2

Summary statistics for adult female queenfish *Seriphus politus* used in analyses of reproductive variables and condition. Gonadal condition (RGI), batch fecundity, and egg diameter variables are least-square means (adjusted for annual differences in the body-size covariate). All variables, including fecundity, refer to sample females only. See Methods for explanations of the covariate used to adjust particular variables. One standard error is given in parentheses below each mean.

Year	N	SL (mm)	Somatic weight (W, g)	RGI[a]	Batch fecundity[b] (no. eggs)	Egg diameter[c] (EU)
1979	44	165	77	3.8	14,752	19.10
		(5)	(7)	(.2)	(1)	(.18)
1980	126	151	56	4.7	15,019	20.61
		(2)	(3)	(.1)	(1)	(.18)
1984	71	137	37	3.9	11,784	20.11
		(2)	(1)	(.2)	(1)	(.23)
1985	77	141	44	5.3	14,550	21.03
		(2)	(2)	(.2)	(1)	(.18)
1986	75	143	44	4.1	14,199	21.10
		(2)	(2)	(.2)	(1)	(.18)

[a] Estimates (± SE) of the exponent "b" in the power equation, gonad weight (G) = aW^b, were 1.185 ± 0.092 (in 1979), 1.162 ± 0.053 (1980), 1.232 ± 0.124 (1984), 1.280 ± 0.102 (1985), and 1.011 ± 0.102 (1986). Estimates did not differ among years, and were consistently greater than one (ANCOVA; ln somatic W × Yr interaction: $F_{4,383} = 0.87$, $P = 0.48$; pooled slope = 1.1810.

[b] Batch fecundity estimates were back-calculated from the means and SE's of ln-transformed data, multiplied by the correction factor of Sprugel (1983).

[c] Using the largest size-class of oocytes (ripe, hydrated-state) present in Gilson's-fixed ovaries (see Methods).

Results

Variations in female body size and CPUE

The size composition of the nearshore, adult female queenfish stock differed among years. Mean female length and weight were significantly lower in 1985 and especially 1984 (Kruskal-Wallis one-way ANOVA; both $P<0.001$). Large females (≥165 mm SL, chosen because they were relatively rare during 1984–86) in fact were nearly absent in 1984, when overall mean female abundance was at an estimated low (Table 1).

Females used in analyses of reproduction and condition also differed in mean body size (both somatic weight and length) among sample years (Kruskal-Wallis ANOVA, both $P<0.001$; Table 2).

Dry vs. wet somatic weight

The dry somatic weight of female queenfish averaged 24% of wet weight for fish collected at the beginning and at the end of the 1985 spawning season. Body length obviously influenced dry weight; subseason, however, had no significant effect on dry weight (ANCOVA of effects of body length and subseason on dry weight: length effect—$F_{1,54} = 346$, $P<0.0001$; subseason effect—$F_{1,54} = 0.42$, $P = 0.52$). Wet weight, therefore, could be used as an accurate proxy for dry weight throughout the queenfish spawning season, once adjusted for variations in female body size.

Batch fecundity

Batch fecundity in queenfish was positively related to female body size in each year (Table 3; Fig. 1). Fecundity was generally better related (based on higher R^2 values) to somatic weight than body length. Batch fecundity was disproportionately large in heavier females, as indicated by the value of the slope in the linear double-log plot (Fig. 1). Fecundity also differed among years, even after adjustment for annual differences in female size, with mean fecundity in 1984 significantly lower (by 20%) than mean fecundity in the other four years (Tables 2, 3, 5; Fig.1).

Table 3

Summary of ANCOVAs[a] testing the effects of female somatic weight and year on batch fecundity (F, no. eggs) and relative gonadal index (RGI). Both model R^2 are significant at $P<0.001$ (ln F, $R^2 = 0.694$; RGI, $R^2 = 0.114$).

Dependent variable	Source	df	*SS*	*MS*	*F*	*P*
ln F	ln W	1	118.1	118.1	693	<0.0001
	Yr	4	3.4	0.8	4.9	<0.0001
	Error	387	65.9	0.2		
RGI	ln W	1	0.06	0.06	0.03	0.87
	Yr	4	111	27.7	12.5	<0.0001
	Error	387	860	2.2		

[a] ln W × Yr interaction terms deleted for analysis of ln F ($P = 0.61$) and for analysis of the RGI ($P = 0.84$).

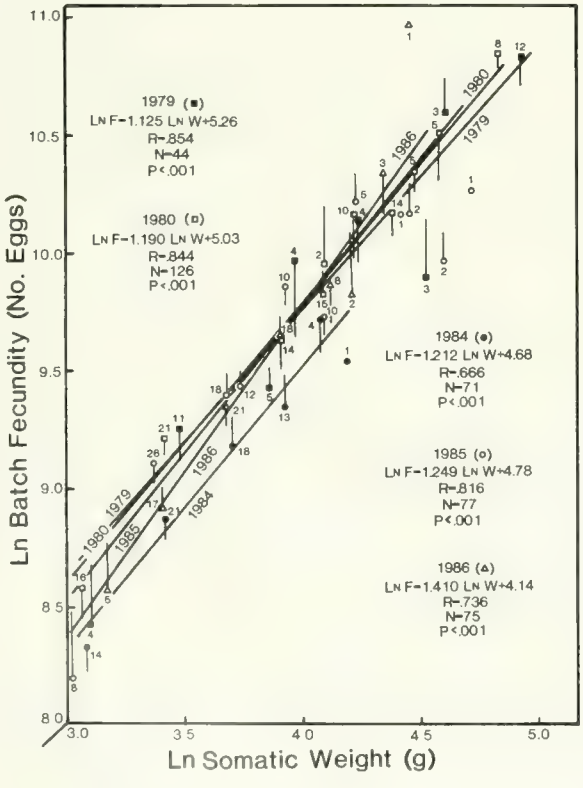

Figure 1

Relationship between the log of batch fecundity (ln F) and log female somatic weight (ln W) during each of the five study years. For illustration, mean fecundity data (+1 SE) are plotted for each 10-g weight class. The allometric equation, $F = aW^b$ (in log-linear form as $\ln F = \ln a + b \ln W$), and its summary statistics are provided for each fitted regression line.

Weight-specific fecundity

Patterns of weight-specific fecundity (WSF, no. eggs per g somatic weight) resembled those of batch fecundity. WSF appeared to increase with female body weight (ANCOVA of effects of somatic weight and year on WSF: weight effect—$F_{1,387} = 13.1$, $P<0.001$), and also seemed to vary among years ($F_{4,387} = 2.84$, $P = 0.025$). However, main effects were confounded by a weakly significant weight-by-year interaction ($F_{4,387} = 2.57$, $P = 0.038$). This heterogeneity of slopes prevented adjustments for annual variations in female weight and invalidated comparisons of intercepts among all five years. Although WSF generally increased with body weight, the disproportionate effect of larger females varied among years. Most notable was the particularly strong, positive influence of somatic weight on WSF in 1986. If the 1986 data are deleted and the ANCOVA analysis rerun, the slope heterogeneity disappears ($F_{3,310} = 0.82$, $P = 0.49$). When main effects are reanalyzed, a strong year effect ($F_{3,313} = 6.02$, $P<0.001$) becomes apparent, in addition to that of somatic weight. This year effect disappears ($F_{3,243} = 0.56$, $P = 0.57$) if the 1984 data are removed. Size-adjusted WSF in 1984 (mean ± SE = 264 ± 15 eggs per g) clearly was less than that in 1979, 1980, and 1985 (336 ± 8 eggs per g).

Diameter vs. dry weight of eggs

The median diameter of Gilson's-fixed, hydrated-state eggs was significantly related to the mean dry weight of these eggs (dry weight [in g, $\times 10^{-6}$] = 7.2 + 0.4931 egg diameter; $r = 0.47$, $n = 46$ females, $P = 0.001$). The mass of hydrated-state eggs therefore was approximately predicted ($R^2 = 0.22$) by egg diameter. While appropriate, I acknowledge that a more direct and

accurate measurement of egg mass would have been preferable.

Egg size

Egg size varied with female body length and period within spawning season, with larger eggs produced by larger females, and all females producing larger eggs earlier in the season (Table 4; Fig. 2). The mean size of eggs did not vary among years, after adjustments for annual differences in female size and a significant period × year interaction (Tables 4,5). The latter interaction illustrates that the pattern of subseasonal decline in egg size varied among years (Fig. 2). Adjusted for female length, mean egg diameter appeared to vary 10% among years (Table 2). This difference in egg diameters, expressed in terms of volume (as 4/3 πr^3, the volume of a sphere), was 35% of the smaller value.

Table 4

Results of two-way ANCOVA testing the effects of female body length (SL, as covariate), study year (spawning season), and bimonthly period within the spawning season on size of ripe ovarian eggs. See Methods for explanation of egg size measurements. Model R^2 (0.510) significant at $P<0.001$.

Dependent variable	Source	df	*SS*	*MS*	*F*	*P*
Egg diameter	SL	1	57	57.0	22.5	<0.0001
	Period	2		{inestimable}		
	Yr	4		{inestimable}		
	Period × Yr	8	226	28.2	11.2	<0.0001
	Error	372	942	2.5		

Table 5

Summary of a posteriori Bonferroni *t*-tests for identity of year effects detected by ANCOVAs summarized in Tables 3 and 4. Means connected by underlines are not significantly different at $P = 0.05$. See Table 2 for values of adjusted means and SEs.

Variable	Year contrasts
ln F	1984 < 1985 = 1986 < 1980 < 1979
Egg diameter	1979 = 1984 = 1980 = 1985 = 1986
RGI	1979 = 1984 = 1986 < 1980 = 1985

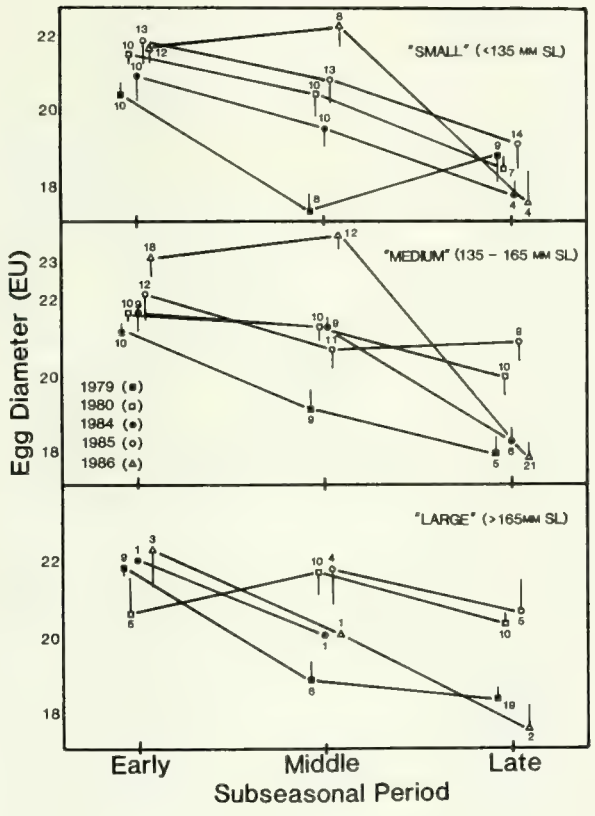

Figure 2

Relationship between mean (±1 SE) egg size (diameter of Gilson's-fixed, hydrated oocytes) and bimonthly period within spawning season for female queenfish of three arbitrary body sizes (small ≤ 13.5 cm, medium 13.6–16.5 cm, and large ≥ 16.5 cm SL), by sample year. See Tables 4 and 5 for results of ANCOVA testing the effects of subseasonal period (within year) on egg size, with female body lengths evaluated as a covariate. Data were pooled by bimonthly period to increase sample sizes.

Condition indices

Somatic condition varied with body size. Larger females usually were more robust (Table 6), but somatic condition also varied among years; the slopes and intercepts of length–weight relations were lower in 1984 and 1985 than in the other three years (Table 6). Larger females in particular were less robust in 1984 and 1985 (i.e., there was a highly significant ln SL × year interaction; Table 6), and this invalidated a straightforward interpretation of the effects of body size and year on a summary index of somatic condition.

As indicated by values consistently greater than one for the exponent "b" in the equation, $G = aW^b$, percentage gonad-to-somatic weight allocation increased for larger females (Table 2; Fig. 3). However, relative

gonadal condition, as described by the RGI of Erickson et al. (1985) in which gonad weight has been standardized by female somatic weight, did not vary with female size (Table 3). The RGI did differ among years in concert with size-adjusted variations in fecundity; mean RGI in 1984 was about 14% lower than the RGI averaged over the other four years (Tables 2, 5). An identical pattern of annual variation in gonadal condition is observed if the classical gonadal index (GSI = [G/W] × 100) is used as the dependent variable in ANCOVA instead of the RGI.

Table 6

Least-squares regression parameters for length-weight relationships of adult female queenfish in each[a] of the study years. Ordinary least-squares regressions were calculated for the double-log transformed equation, $\ln W = \ln a + b \ln SL$, where ln a is the intercept and b is the slope.

	Intercept		Slope				
Year	Estimate	SE	Estimate	SE	R^2	N	P
1979	−11.864	0.246	3.151	0.048	0.990	44	<0.0001
1980	−11.660	0.178	3.106	0.036	0.984	126	<0.0001
1984	−10.450	0.378	2.853	0.077	0.952	71	<0.0001
1985	−10.433	0.206	2.862	0.042	0.984	77	<0.0001
1986	−11.888	0.616	3.152	0.124	0.898	75	<0.0001

[a]Estimated slopes of the ln W − ln SL relations differed among years (ANCOVA; ln SL × Yr interaction: $F_{4,393} = 6.10$, $P<0.0001$).

Potential biases of condition indices

These differences in somatic and gonadal conditions were not the result of year variations in condition-selective collection methods. Lampara-seined fish comprised 84–100% of the specimens examined for condition in each year; among non-lampara fish, a maximum of 14% of the fish examined (in 1984) were collected by otter trawl. The somatic conditions ($K = 10^5 W/SL^3$; Le Cren 1951) of fish collected by lampara seine and otter trawl during April–June 1984, the only period when testable numbers of fish were collected using more than one method, were indistinguishable (seine: mean ± SE condition = 1.40 ± 0.016; trawl: mean ± SE = 1.39 ± 0.010; Student's $t = 0.28$, df = 151, $P = 0.78$).

Discussion

Annual variations in body size

Interannual variations in the body size of adult female queenfish were marked, with the percentage contribution of large fish varying tenfold and mean somatic weights of the nearshore female stock varying by 25% over the study period. Clearly, potential year effects on fecundity and other size-sensitive variables are confounded with the effects of annual variations in body size, necessitating the use of size as a covariate in analyses.

Fecundity and female body size

During each of the queenfish spawning seasons monitored, batch fecundity was positively related to female body size, especially somatic weight. The overall mean value of b in the equation, $F = aW^b$ was 1.2087, which is significantly greater than unity.

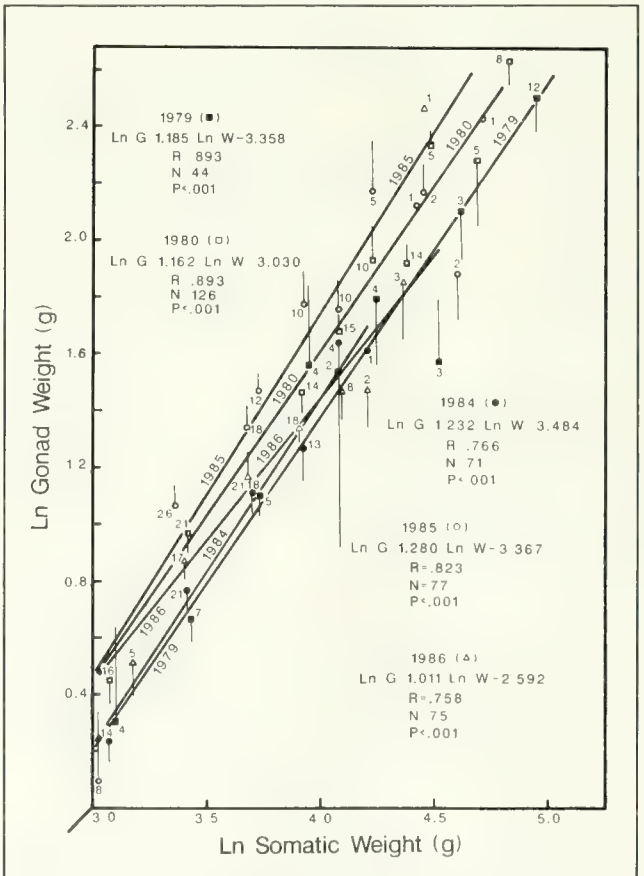

Figure 3

Relationship between the log of ovary weight (ln G) and log female somatic weight (ln W) during each of the five study years. For illustration, mean ovary weight data (+1 SE) are plotted for each 10-g weight class. The equation, $G = aW^b$ (in log-linear form as $\ln G = \ln a + b \ln W$), and its summary statistics are provided for each fitted regression line.

In another detailed study, Parrish et al. (1986) detected allometric weight-specific fecundities in a size-(age-) structured stock of the northern anchovy. Empirical data for additional species of "weedy" (fast-growing, high-fecundity) fishes suggest that allometric fecundity-weight relations may be a general phenomenon (Blaxter and Hunter 1982, Clarke 1987). Reiss (1987), in a review and interpretation of relevant data, calculated that larger (older) fish in general have disproportionately large reproductive investments. Williams (1966), Wootton (1979), and Reiss (1987) have argued that disproportionate investments by older individuals should be adaptive for many iteroparous fishes with indeterminate growth. The queenfish data further suggest that allometry in gonadal allocation may be more common than is generally appreciated. Adjustments for allometry are required when calculating egg-based stock size estimates for species like queenfish and northern anchovy (Parrish et al. 1986).

Covariates of egg size

Egg size was positively related to queenfish body length, but declined for females of all sizes as water temperatures increased between the beginning (March–April) and end (July–August) of the spawning season. Egg size has been observed to increase with female body size, and decreases in egg size have been related to increases in water temperature during spring–summer production cycles, for diverse marine fishes (Williams 1967, Ware 1977, Blaxter and Hunter 1982 and references, Kashiwagi et al. 1985, Knutsen and Tilseth 1985, Daoulas and Economou 1986 and references, Imai and Tanaka 1987, Tanasichuk and Ware 1987). A positive female size–egg size relation and a seasonal decline in egg size with increasing water temperatures, the latter either ecophenotypic or genetic responses to the changing prey or predator (Clarke 1989) spectra confronting larvae, are now recognized as general phenomena in marine pelagic-spawners (Ware 1975; Markle and Frost 1985). It is obvious that estimates of mean egg size (and fecundity) must account for the effects of female body size and subseasonal variation.

Annual variations in fecundity and egg size

Batch fecundities of queenfish (adjusted for annual variations in female size) varied less than 6% during four out of the five years of this study. A marked change in batch fecundity, after adjustments for variations in female size, occurred only in 1984. Weight-specific fecundities paralleled batch fecundities.

Queenfish egg size varied little among the five years studied. Apparent egg volume averaged about 24% smaller in 1979 than during the other four years.

Few data exist on annual variations in the egg production of marine fishes (Bagenal 1957 and references, Antony Raja 1971, Pinhorn 1984, Hunter et al. 1985, Bailey and Almatar 1989). As one might expect, the size-specific fecundity of individuals varies among years, but sometimes fecundities are remarkably similar within a short series of years (Antony Raja 1971, Pinhorn 1984, Hunter et al. 1985). Observational and experimental studies (e.g., Tyler and Dunn 1976, Wootton 1979, Hunter and Leong 1981, Hay and Brett 1988) demonstrate that fluctuations in fecundity can and do result from naturally occurring food limitation. Food rations can also affect egg size (Hislop et al. 1978, Le Clus 1979). The trivial inference is that food can sometimes, although not invariably, limit egg production. Of greater interest is that, for queenfish, the maximum observed deviation from long-term average fecundity was only a 20% decline in a single year of unique oceanographic conditions, as described in the following section.

El Niño effects

The anomalously low fecundities and somatic condition of queenfish in 1984 occurred at a time when the 1982–84 El Niño was still evident in the Southern California Bight (McGowan 1985). During 1983–84, zooplankton production was at unusually low levels in inner-shelf waters (Petersen et al. 1986), mirroring the nadir in phyto- and zooplankton production in the California Current, farther offshore (McGowan 1985). This decline in planktonic production off southern California lagged the more extreme declines in production that resulted from the parent El Niño that occurred off the western coast of South America during 1982–83 (Barber et al. 1985).

During the 1982–84 California El Niño, tropical pelagic fishes migrated northward; many species became abundant off southern California, with some noted as far north as Washington–British Columbia (Smith 1985, Mysak 1986). El Niño effects on subtropical and cold-temperate fishes are poorly understood. Bailey and Incze (1985) and Mysak (1986) summarized the fragmentary data then available on distributional shifts and fluctuations in stock sizes of temperate fishes. Bailey and Incze (1985) speculated that El Niño effects on water temperature, nutrients, and planktonic production could effect egg and larval physiologies, disrupt the transport of early-life-history stages, and impact the somatic condition and egg production of adults. For vagile species, major impacts such as these should prompt movements to regions more favorable for growth and reproduction (Bailey and Incze 1985).

My data on interannual variations in body size composition suggest that large female queenfish (those individuals whose somatic condition and reproduction were particularly stressed by reductions in their anchovy prey) responded to El Niño conditions in part by emigrating out of the study area. The observed 1984 nadir in females >165 mm, followed by the return of fish of this size in 1985–86, demonstrates that emigration had to have occurred, because 165-mm long queenfish are more than 3 years-old (E. DeMartini, unpubl. data). Large fish might have emigrated to deeper depths, tracked colder water masses upcoast, or done both; unfortunately, lack of data prevent discrimination among these possibilities.

The only published evidence thus far for El Niño effects on adult fish condition and egg production off the west coast of North America are for the central stock of the northern anchovy (Fiedler et al. 1986), yellowtail rockfish *Sebastes flavidus* (Lenarz and Echeverria 1986), and for Pacific herring *Clupea harengus pallasi* (Tanasichuk and Ware 1987). In anchovy, individual egg production was lower in 1983–84 than in 1980–82 and 1985; this reflected lower spawning frequencies more than declines in batch fecundity (Fiedler et al. 1986). Specific fecundity (the daily production of eggs per unit biomass) of anchovy was low in 1983 (although high in 1984, the second El Niño year) compared with other years between 1980 and 1985. Growth rates of juvenile–adult anchovy were low in 1983–84 (Fiedler et al. 1986). For yellowtail rockfish off the central California coast, the visceral fat and gonad volumes of adults were lower in 1983 than in 1980 (Lenarz and Echeverria 1986). Off British Columbia, Pacific herring responded to the El Niño with increased batch fecundities coincident with reductions in mean egg size (Tanasichuk and Ware 1987). Adults of the anchovy and rockfish do not regularly occur in inner-shelf waters: most anchovy frequent the California Current, tens to several hundred kilometers offshore of central and southern California. Adult yellowtail rockfish are an epibenthic predator of continental borderlands offshore of the coasts of British Columbia–California.

It is tempting to speculate that the observed decrease in fecundity and somatic condition of queenfish during 1984 reflects lower production of the planktonic and anchovy prey of adults during a major El Niño year, compared with the 1979–80 and 1985–86 periods. If true, these data are among the first to show annual variations in egg production resulting from differences in size-specific batch fecundity, rather than changes in the duration of the spawning season or changes in the spawning frequency of females (Hunter et al. 1985). Interestingly, queenfish egg mass was not detectably lower in 1984, concurrent with the 20% decline in the number of eggs produced per batch, so the impact on egg production may have involved only the quantity, not the quality of eggs. Total number of spawnings per female season, whether due to changes in the duration of the spawning season or frequency of spawning by individual females, also might have varied for queenfish during 1979–86, but data are lacking. Length of spawning season and the interval between batches are unlikely to cancel out the batch fecundity pattern, though, since they might be expected to vary in concert with fecundity, if they covary at all (Hunter et al. 1985).

My observations also provide one of the first suggestions of food web impacts of the 1982–84 California El Niño on an inner-shelf fish species. Unfortunately, data on potential El Niño effects on the survivorship of early-life stages and year-class establishment are lacking for queenfish, as for offshore fishes. Future studies should concurrently measure survivorship and recruitment, together with population fecundity and egg production of the stock, in addition to individual fecundity and condition.

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Abstract.– Age and growth of the school shark *Galeorhinus galeus* was studied from rings in the vertebra and length-frequency data. Samples were collected by trawling off the southern Brazilian coast from June 1980 to September 1986. Histological studies were also conducted on the characteristics of the vertebra. Standard histological techniques and microradiography were used to determine the pattern of vertebral calcification. The vertebrae of *G. galeus* are composed of calcified cartilage. Chondrocytes in calcified zones remain alive, probably nourished through vascular channels extending from the perichondrium into the cartilage matrix. A narrow zone of uncalcified matrix at the outer edge of the centrum indicates that calcification is preceded by initial development of hyaline cartilage. The vertebra presents a pattern of alternating heavily and less heavily mineralized zones, narrow and wide, respectively. The narrow zones were named rings, which are translucent under transmitted light and white to the microradiograph. These rings are probably laid down yearly in a slow-growing phase extending throughout the four winter months of June to September. Lengths at age were back-calculated and the von Bertalanffy growth parameters are: males—$K = 0.092$, $L_\infty = 152$ cm, and $t_0 = -2.69$; females—$K = 0.075$, $L_\infty = 163$ cm, and $t_0 = -3.00$. ELEFAN software was used to determine the growth curve best fitted to length-frequency data, but results overestimated the growth rate due to the slow growth and modal overlap.

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Age, Growth, and Structure of Vertebra in the School Shark *Galeorhinus galeus* (Linnaeus, 1758) from Southern Brazil

Beatrice Padovani Ferreira

Fundacao Universidade do Rio Grande, Rio Grande, RS, 96200, Brazil
Present address: Marine Biology Department
James Cook University of North Queensland, Townsville Q4811, Australia

Carolus Maria Vooren

Departamento de Oceanografia, Fundacao Universidade do Rio Grande
Rio Grande, RS, 96200, Brazil

The elasmobranch skeleton consists of calcified cartilage. In most elasmobranchs, vertebrae are the only available structure that display periodic rings, which are useful for determining age. These rings result from different ratios of organic matrix/mineral, making the zones optically distinct (Casselman 1974). Since the description by Ridewood (1921), several techniques have been developed for enhancing the visibility of these rings thus making the counts easier and more accurate. However, information about the histology of elasmobranch vertebral rings is limited, and statements about their chemical composition and optical properties are contradictory (Casselman 1983).

The school shark *Galeorhinus galeus* is one of the principal species in the shark fishery in southern Brazil (Vooren and Betito In press). With the purpose of providing information for management decisions, age and growth of the Brazilian school shark were determined from rings in the vertebrae and length-frequency data. A histological study was conducted to investigate the structure of the vertebrae and to determine variations in their composition.

Materials and methods

The study area was the continental shelf and upper slope off southern Brazil, between latitudes 34° and 30°S, at depths between 10 and 500 m. Data used for size-frequency analysis were obtained during trawl fisheries of this area from June 1980 to September 1986 (Table 1). All fishes were sexed and their total length (TL, cm) was measured from the tip of the snout to the extremity of the upper lobe of the tail, which was stretched back to be aligned with the body axis. Vertebrae were collected during the cruises listed in Table 1, and samples were chosen to include both sexes and the full size-range available. Sexual maturity and reproductive stage (Table 2) were determined according to size criteria established for this species by Peres (1989).

The data were processed on the Statistical Package for the Social Sciences, SPSS (Nie 1975). Length-frequency distributions for both sexes were plotted by cruise, by month, and also by a selected combination of the two largest samples. The ELEFAN (Electronic Length Frequency Analysis) software (Pauly and David 1981) was used to determine growth parameters (k and L_∞) from length-frequency data. The goodness of fit was given by the index Rn.

Vertebrae for age determination were dissected in the field from the

region under the first dorsal fin. The vertebrae were cleaned, frozen, and preserved in 70% ethanol. Several techniques were tried to aid enhancement and interpretation of the vertebral rings. Vertebrae of 10 sharks were sectioned into two halves, through transverse or sagittal planes, and the exposed faces were polished on wet 600-grit sandpaper. They were decalcified in 1% formic acid for 1 hour, rinsed in running water for 24 hours, dried and stained with graphite powder. The material was observed with a dissection microscope at 10× magnification using reflected light.

Vertebrae from 82 individuals (35 males, 45 females, and 2 embryos) were dehydrated in ethanol, cleared in styrene, embedded in polyester resin, sectioned with a jeweller's saw in transverse and sagittal planes, and polished on wet 400-grit sandpaper to obtain slices of 50–250 microns. Radiographs of all sections were taken with Soft X-ray equipment by Moureuil (France), at settings of 10–30 kV, 5–15 mA, and exposure times of 3–5 minutes. Kodak Industrex M radiography film was used. The radiographs were mounted on glass slides as were vertebra sections, either directly or after staining with Harris's haematoxylin or basic fuchsin. Vertebrae from five sharks were prepared and sectioned by standard histological techniques for calcified material. Sections were stained with Sudan 4 for observation of the lipid contents of cells.

A dissecting microscope at 10× magnification was used for measuring and counting growth rings, and a compound microscope at 100× magnification for observation of cell structure and details of the margin of the vertebra. The criteria to define a ring requires that it must occupy a distinct translucent zone relative to adjacent opaque zones and that the ring traverse the corpus calcareum and intermedialia (modified from Casey et al. 1985).

Measurements of growth increments were made with an ocular micrometer positioned to measure distances from the focus (notochordal remnant) to successive growth bands. The radius of each centrum was measured from the focus to the distal margin of the corpus calcareum (Fig. 1). The widths of individual translucent and opaque zones were measured in the microradiographs of 10 individuals. The periodicity of the formation of the rings was studied by examining the margins of the vertebrae collected from June to September. The marginal zone was classified into three types: pre-ring, consisting of a wide, less calcified zone; ring, consisting of a more calcified zone; and post-ring, consisting of a narrow, less calcified zone. Measurements of marginal increments were considered to be ineffective because the widths of zones varied greatly between size classes.

A linear regression of TL as a function of centrum radius was fitted to the data for juveniles and adults (sexes combined and separate) and the equality of

Table 1

Catch data of *Galeorhinus galeus* during cruises conducted by the NOc *Atlantico Sul*. Asterisks indicate vertebrae collected.

Cruise code/year (month)	Sites	Latitudes (min.–max.)	Depth (m)	Male (n)	Female (n)
3/80 (June)	1	— —	120	19	370
4/80 (July)	1	— —	—	65	94
7/80 (Sep.)	7	30°44′–35°52′S	120	108	114
*7/81 (Sep.)	5	— —	—	55	161
9/81 (Sep.)	8	30°36′–34°24′S	120	184	276
3/82 (July)	10	— —	—	491	160
10/83 (Aug.)	7	30°42′–34°22′S	100	—	30
3/83 (Nov.)	14	30°44′–34°16′S	160	43	36
*4/84 (June)	15	— —	—	301	230
2/85 (June)	7	— —	—	72	104
*3/85 (July)	23	— —	—	76	101
*4/86 (July)	12	32°00′–34°00′S	500	65	414

Table 2

Sexual maturity of *Galeorhinus galeus* determined by size class. Data from Peres (1989).

	Total length (cm)	
	Males	Females
Juveniles	43–88	43–103
Adolescents	93–108	108–123
Adults	113–143	128–153

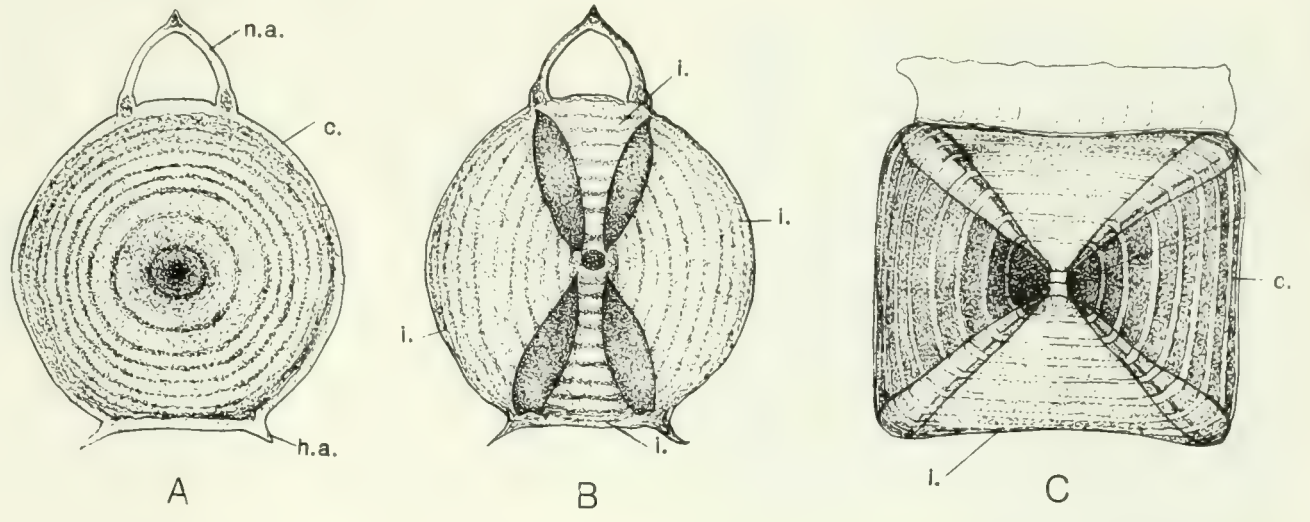

Figure 1

Drawings of *Galeorhinus galeus* vertebrae showing patterns of calcification in centra. (A) View from end of centrum toward focus, showing growth rings; (B) view at center of centrum, showing Maltese Cross of calcified radialia; (C) longitudinal view showing double cones and growth rings. c = centrum, h.a. = haemal arch, i = intermedialia, n.a. = neural arch.

slopes of the regression lines tested (Sokal and Rohlf 1981). As they were found to be different, a power relationship was fitted to TL × centrum radius for each sex. Each ring was measured and these values inserted into the power equation to back-calculate the length of each shark at formation of the respective ring. The von Bertalanffy growth model was fitted to the mean lengths-at-age, using the methods of Ford and Beverton as cited by Gulland (1977).

Results

Size composition

School sharks were present in the study area from April to November. During April and May all captured individuals were adolescent or adult gravid females (Fig. 2). From June to September the largest captures were registered (Table 1) and individuals from both sexes and all sizes (43–148 cm) were present (Figs. 2, 3). Larger juveniles were still captured during September, but individuals smaller than 70 cm TL were caught only from June to August.

A size variation within the sample size composition was also observed when analyzing the length frequencies plotted by cruise (Figs. 4, 5). Some size classes were better sampled during certain cruises. For instance, the sample was mainly composed of adults during cruises 3/80, 7/80, and 4/86, and of juveniles

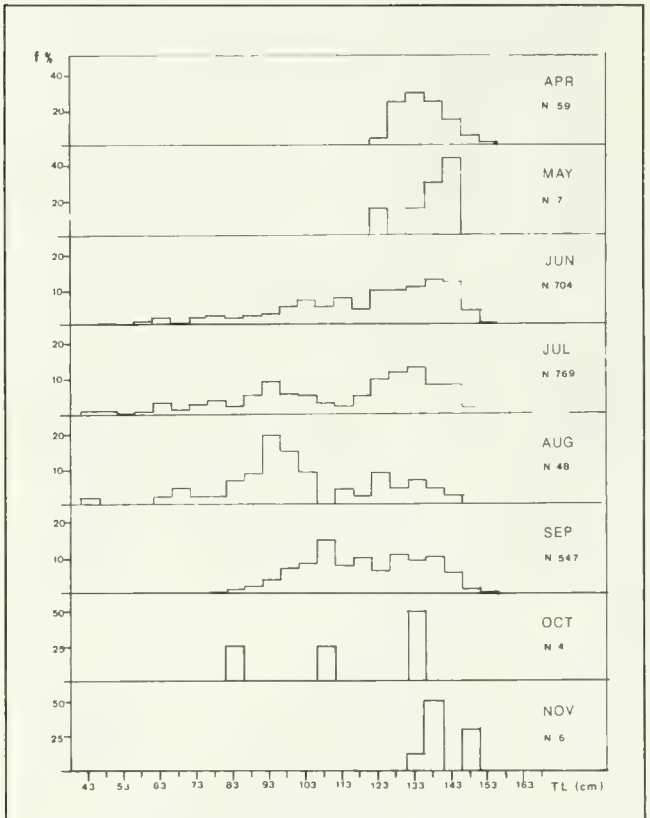

Figure 2

Length-frequency distribution of female *Galeorhinus galeus* by month.

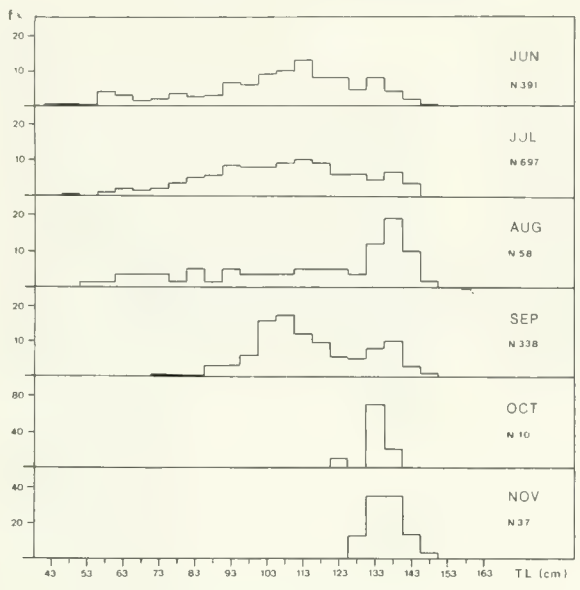

Figure 3
Length-frequency distribution of male *Galeorhinus galeus* by month.

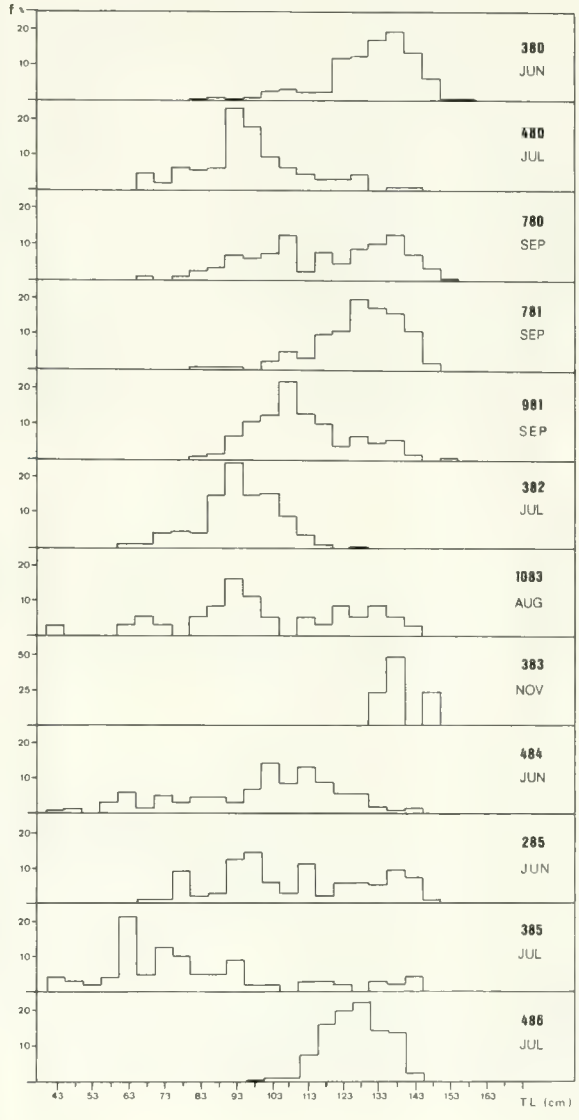

Figure 4
Length-frequency distribution of female *Galeorhinus galeus* by cruise.

during cruises 4/80, 9/81, and 3/82. Smaller length classes were more frequently caught during cruises 4/84 and 3/85, but did not form a marked mode in the length-frequency distribution.

Techniques for enhancing vertebral rings

Rings were visible in all the attempted methods, but because of the large number of rings and marginal crowding in the centra of older sharks, only detailed microscopic observations were successful in providing comprehensive readings and measurements. The graphite method was an easy and simple technique that provided good results in enhancing rings of vertebrae of younger sharks. However, the large number of rings near the margin of vertebrae of older sharks was difficult to determine using this technique, and the number of rings was always underestimated compared with results by other techniques.

Stained sections of vertebrae provided good results in enhancing rings both in calcified and decalcified material. In the latter, no measurements were taken because of shrinkage and distortions observed after the decalcification procedure. The matrix shrank in the space formerly occupied by the mineral, and this zone became narrower than in the calcified state.

The most satisfactory technique for enhancing and counting rings was microradiography. With this method, the more calcified zones appeared white while the less calcified appeared dark (Figs. 6, 8). Direct observations of the sections showed that the former more mineralized zones were translucent and the latter less-mineralized zones were opaque when observed under transmitted light (Figs. 7, 8). Sections of various thickness were examined. The best contrast between zones was obtained from sections between 250 and

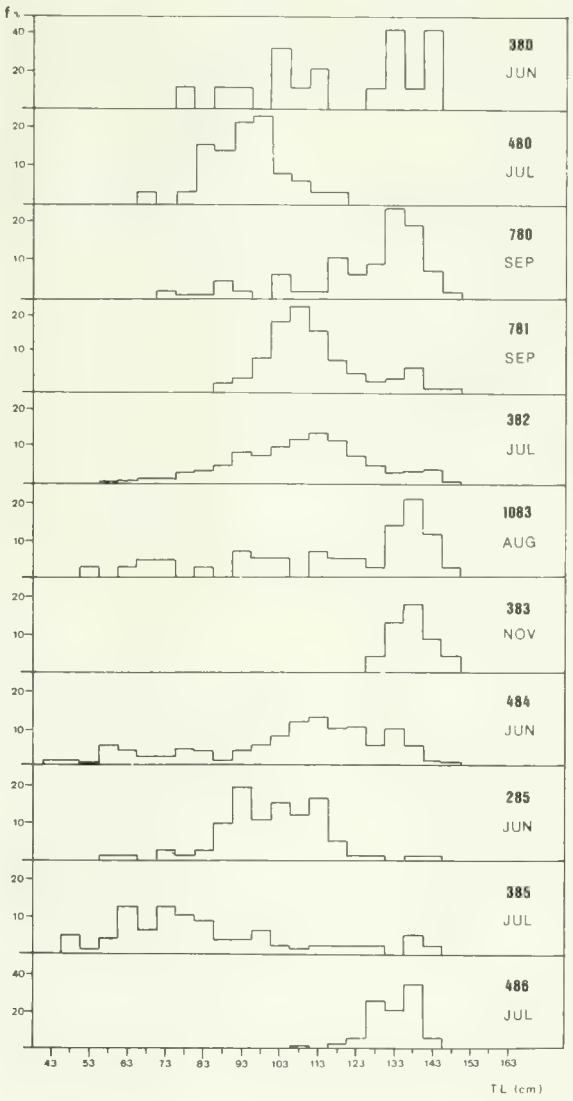

Figure 5
Length-frequency distribution of male *Galeorhinus galeus* by cruise.

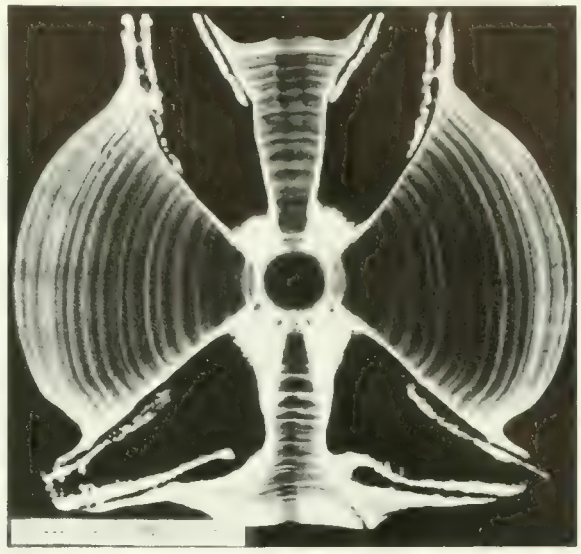

Figure 6
Microradiograph of transverse section of *Galeorhinus galeus* vertebra.

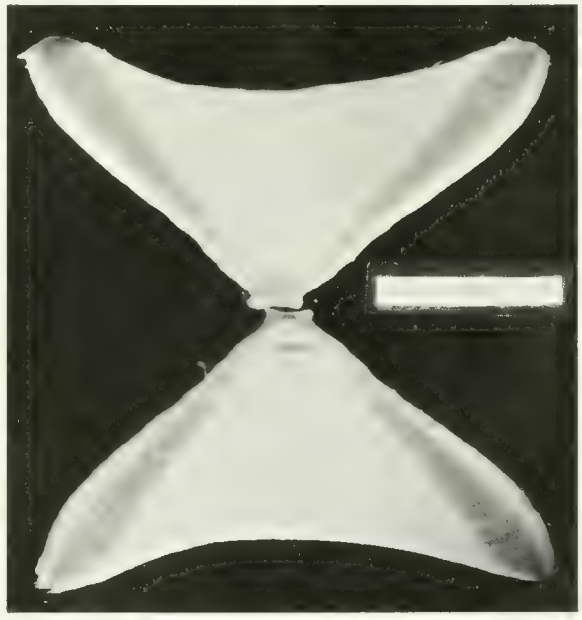

Figure 7
Sagittal section of *Galeorhinus galeus* vertebra under reflected light with dark background. Translucent zones appear dark and the opaque zones appear white.

750 μ for readings of interior rings and from 50 to 100 μ thick for readings on the margins.

Pattern of vertebral calcification

The vertebra of *Galeorhinus galeus* is composed of calcified cartilage. Its centrum consists of a corpus calcareum of two obtuse, hollow cones with their apices joined and opposed. The space around the two cones is organized into four oblique basalia and four calcified intermedialia: dorsal, ventral and lateral (Fig. 1) (Goodrich 1958, Ridewood 1921). In transverse section through the center of the centrum (focus), these radial

calcifications within the basalia have the shape of a Maltese Cross (White 1937) (Figs. 1B, 6). This "carcharinoid" pattern is characteristic of the families Triakidae, Sphyrnidae, and Carcharhinidae (Applegate 1967). Above the centrum is a neural arch. In the center of the centrum is a hole, marking the position of the primitive notochord, which we adopted as the focus of the vertebra. Within each cone, the focus is surrounded by a series of concentric rings which are read through techniques using the whole centra.

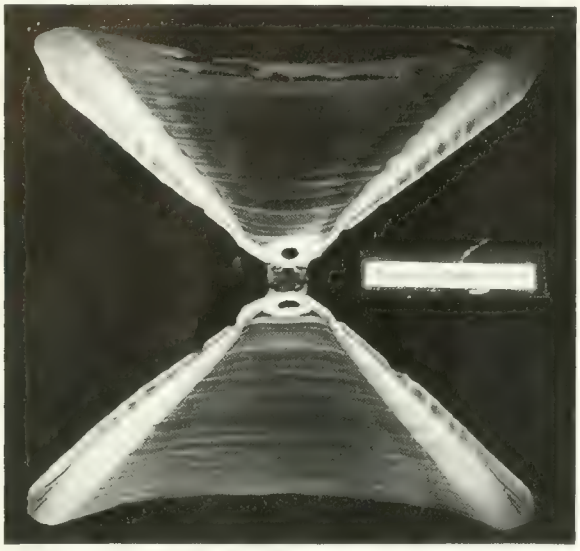

Figure 8
Microradiograph of sagittal section of *Galeorhinus galeus* vertebra from Figure 7. The more calcified zones (rings and cone in general) appear white, and the less calcified zones (opaque zones and intermedialia in general) appear dark.

The inside of each cone is lined by a perichondrium, which consists of a fibrous layer covering a germinative layer of chondroblast cells (Fig. 9). During growth phases, the chondroblasts differentiate into chondrocytes to form the mature cartilage, a densely cellular tissue consisting of rounded cells embedded in their secreted organic matrix. The body of the vertebra forming the intermedialia is also invested by a perichondrium. In sagittal section the differences between the two regions can be observed: the cells of the cone are smaller and embedded in a more abundant matrix than those of the intermedialia (Fig. 10). Mineralization occurs throughout the matrix and both regions present an alternate pattern of more and less mineralized zones, corresponding to the concentric rings that can be seen inside the cone.

The properties of the narrow and wide zones, which occur in an alternating sequence, were defined by comparing microradiographs and direct observations with transmitted and reflected light of sections of the same vertebra. In this species the narrow zone, which we define as a ring, is optically translucent and appears white on the radiograph, being opaque to the X-ray beam, and therefore more calcified. The wide zone, defined here as a growth zone, is optically opaque and appears dark on the radiograph, being semi-transparent to the X-ray beam, and therefore less calcified (Figs. 7, 8).

Figure 9
Sagittal section of *Galeorhinus galeus* vertebra showing part of the cone and intermedialia. Starting from external side: a = perichondrium; b = ring crossing cone; c = ring crossing intermedialia. (Harris's haematoxylin, 100×)

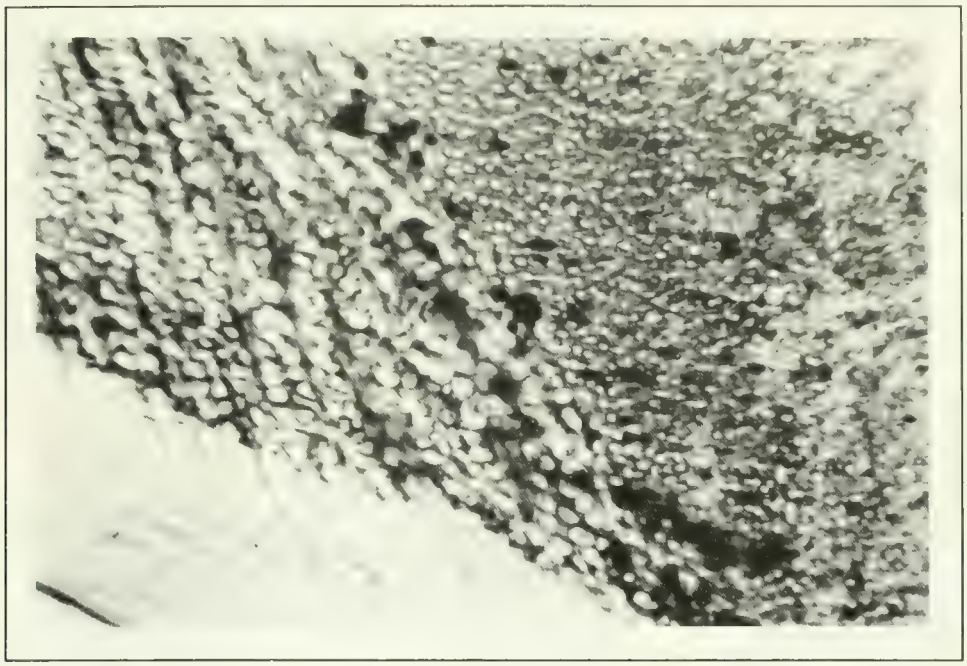

Figure 10
Sagittal section of *Galeorhinus galeus* vertebra showing contrasting tissue of cone and intermedialia. (Harris's haematoxylin, 100×)

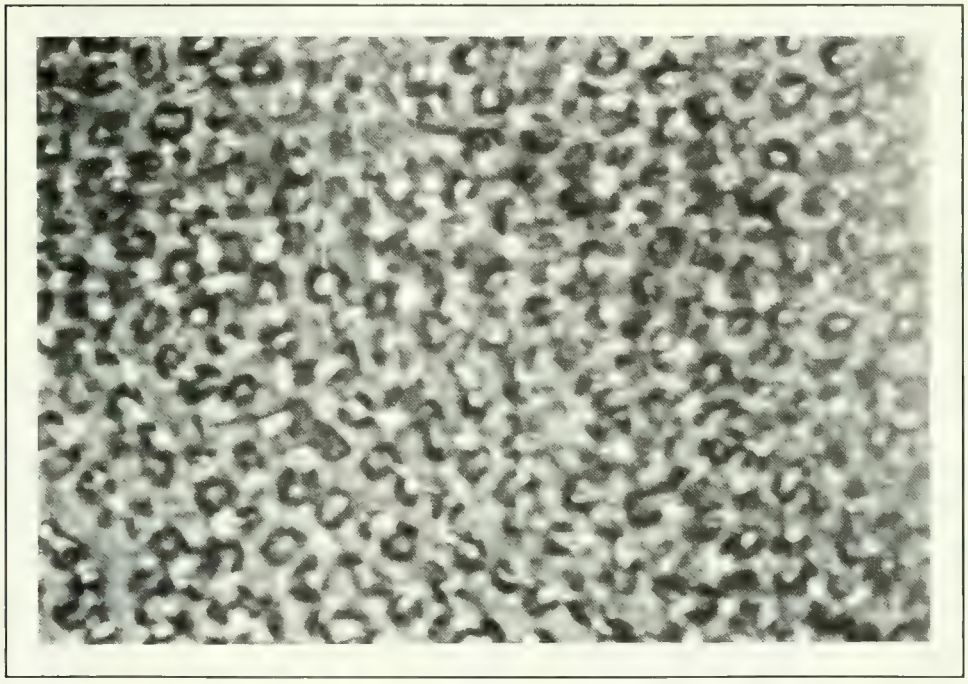

Figure 11
Section of vertebral tissue of *Galeorhinus galeus* showing the thin channels linking the cells. (Harris's haematoxylin, 400×)

Thin vascular channels connecting the cartilage cells were observed in haematoxylin-stained sections of resin-embedded vertebrae. These canaliculi form a network in the matrix between cells providing an opportunity for fluids and nutrients to reach the interior from the external medium (Fig. 11). Absence of lipid inclusions in the chondrocytes is interpreted as evidence of a healthy and active cellular metabolism. The presence of isogenic groups of cells suggests that cells divide interstitially and thus effect interstitial growth.

The widths of translucent and opaque zones varied in individuals. Rings were usually narrower than adjacent opaque zones, but with increased body size (TL), both attained the same average size (Figs. 12, 13). Width of a male's opaque zones decreases gradually, and after about the 15th ring the two zones are equal

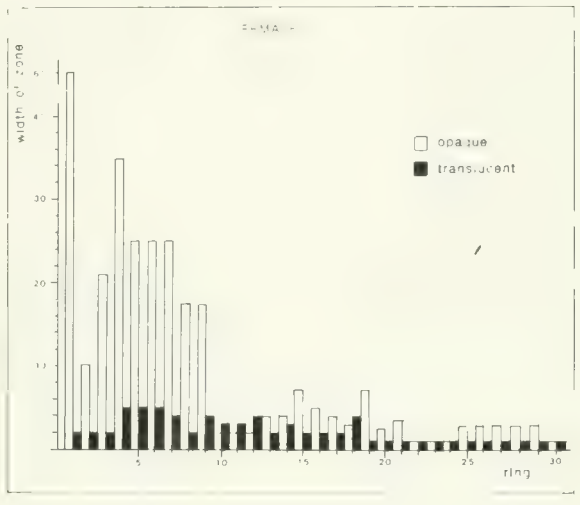

Figure 12
Widths (m.u. = 10^{-3} cm) of translucent and opaque zones distributed by ring for female *Galeorhinus galeus* (134 cm TL, 29 yrs-old).

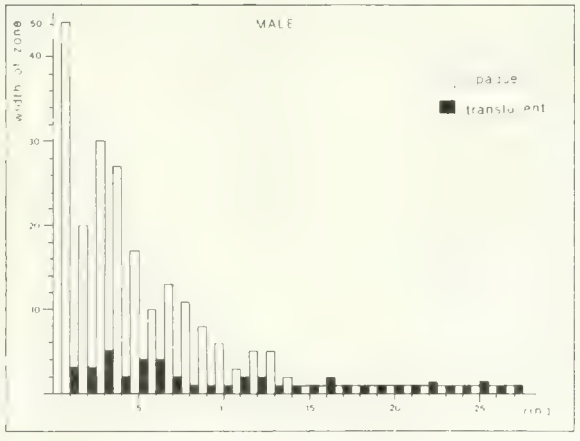

Figure 13
Widths (m.u. = 10^{-3} cm) of translucent and opaque zones distributed by ring for male *Galeorhinus galeus* (141 cm, 26 yrs-old).

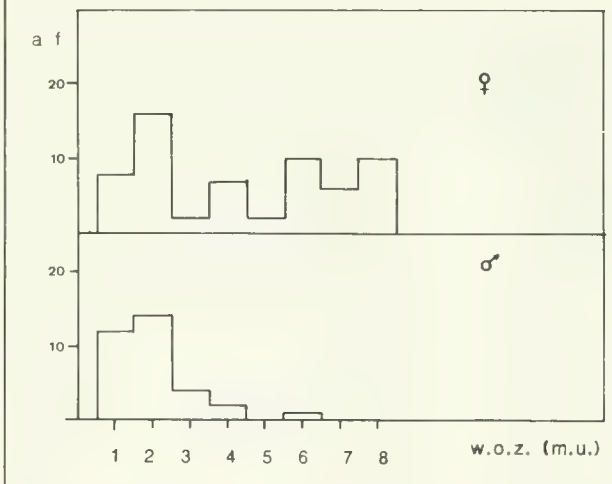

Figure 14
Frequency distribution of widths of opaque zones after the 15th ring for female and male *Galeorhinus galeus*.

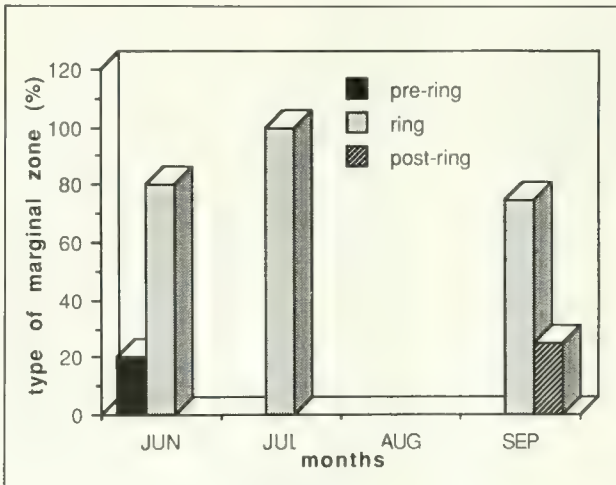

Figure 15
Percentage of type of marginal zone in vertebrae of *Galeorhinus galeus* observed June–September ($n = 82$).

in width. Females have the same general pattern, but some variation in width still can be detected after the 15th ring has been formed (Fig. 14).

From June to September, 91% of the vertebrae examined showed more calcified zones forming at the margins (Fig. 15). During June this percentage was 80%, rising to 100% during July and falling to 75% in September. The vertebrae observed with less calcified zones at margins during June (20%) were of the pre-ring type (wide less-calcified zone), and the ones observed during September (25%) were of the post-ring type (narrow less-calcified zone). These results indicated that the ring formation probably occurred during the winter months (June to September). One mark per year seems to be the most likely case for the school shark, and results here reflect this assumption.

In vertebrae of embryos at 8 months of intrauterine age, only the cartilage of cones was mineralized and no rings were visible (Fig. 16). Their intermedialia was

formed by a hyalin, unmineralized cartilage (Fig. 17). A 45cm TL juvenile shark's vertebra showed some mineralization of the intermedialia, but unmineralized areas were still present. Two rings were observed (Fig. 18). The first ring was probably formed during the first winter after the birth in November (Peres 1989). The most recent one was just forming on the margin. In adult individuals the largest number of rings was 41, observed in a female of 155cm TL.

Histological observations revealed the presence of a thin uncalcified layer at the very edge of the vertebrae, peripheral to the outermost narrow or wide calcified zones at the margin (Fig. 18). This indicates that the marginal growth of the vertebra starts with the formation of an unmineralized layer of cartilage which is subsequently mineralized. This layer is probably present throughout the year and does not by itself indicate periodicity of ring formation.

Figure 16
Microradiograph of a sagitally sectioned vertebral column from a *Galeorhinus galeus* embryo, showing calcification (white zones) of double cone in centrum (50×).

Back-calculation

All linear regressions of total length on vertebral radius were significant ($p<0.05$). The regression slopes were significantly different between juveniles and adults ($p<0.05$) and between adult males and females ($p<0.05$). Therefore, a power relationship was found to be more adequate to fit the pooled data for juveniles and adults of each sex. The following equations were obtained: Females ($N=26$), $TL = 32.59 \times R^{0.827}$ and males ($N=33$), $TL = 25.07 \times R^{0.897}$, where N indicates sample size and R radius of vertebra, with TL in cm and R in micrometric units (1 m.u. = 10^{-3} cm) (Fig. 19).

Lengths were back-calculated by age class and did not reveal the occurrence of Rosa Lee phenomenon (Gulland 1977), so the lengths at age were averaged (Table 3). The von Bertalanffy growth parameters were: females, $k = 0.075$, $L_\infty = 163$cm, and $t_0 = -3.00$; males, $k = 0.092$, $L_\infty = 152$cm, and $t_0 = -2.69$. The growth curves calculated from these parameters are shown in Fig. 20.

Using the ELEFAN software, several attempts were made to find the growth curve best fitted to the length-frequency data. In order to obtain a data set contain-

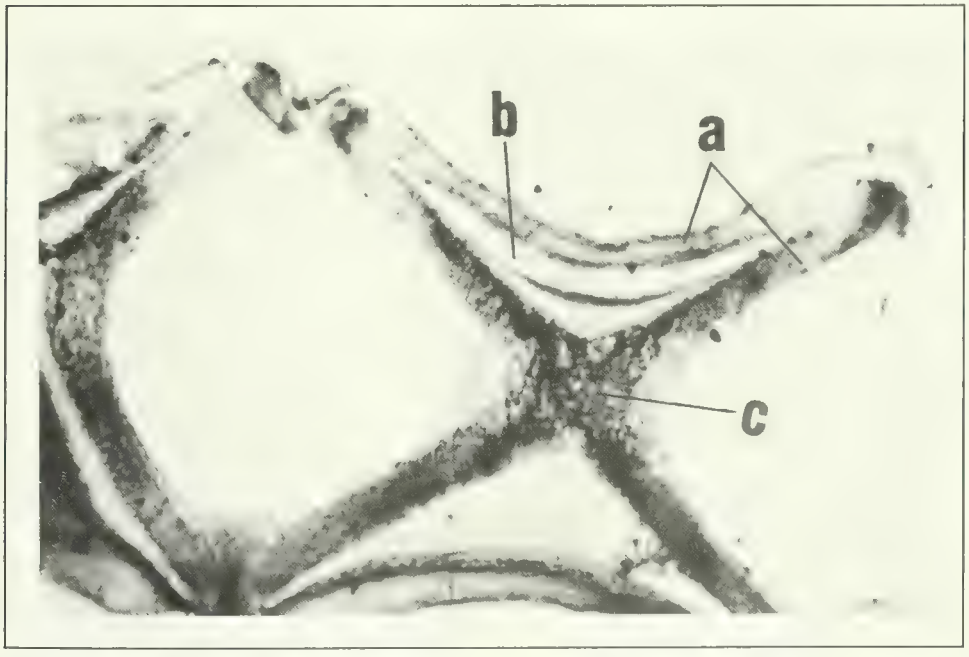

Figure 17
Sagittal section of vertebra from a *Galeorhinus galeus* embryo, showing (a) perichondrium, (b) hyaline cartilage in intermedialia, and (c) calcified cartilage of cones. (Haematoxylin, 100×)

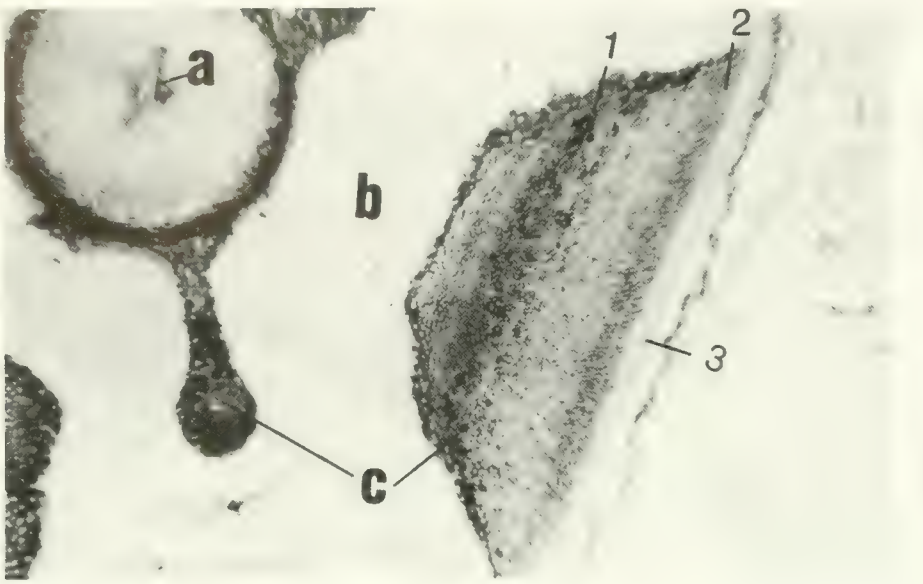

Figure 18
Portion of a transverse section of a vertebral centrum from a 2d-year *Galeorhinus galeus* juvenile, showing (a) focus, (b) hyaline cartilage, and (c) calcified cartilage of intermedialia. (1) 1st ring, (2) 2d ring, and (3) uncalcified margin. (Haematoxylin, 50×)

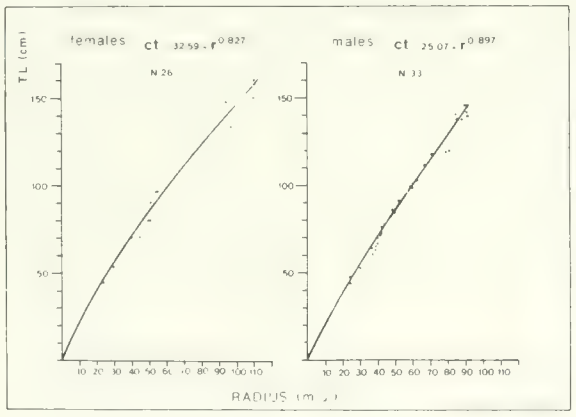

Figure 19
Relationship between total length and vertebra radius (R) for female and male *Galeorhinus galeus* (m.u. = 10^{-3} cm).

Table 3
Back-calculated lengths (TL, mm) at age for male and female *Galeorhinus galeus*.

Age (years)	Ring	Male (*n*)	Male TL	Female (*n*)	Female TL
0	1	18	343	18	323
1	2	17	464	18	424
2	3	16	545	17	496
3	4	16	616	15	579
4	5	12	693	13	668
5	6	12	762	11	747
6	7	8	818	10	818
7	8	5	893	9	890
8	9	4	947	9	946
9	10	4	998	9	992
10	11	4	1027	8	1037
11	12	4	1070	6	1048
12	13	3	1137	4	1091
13	14			4	1123
14	15			4	1152
15	16			2	1196
16	17			2	1215
17	18			1	1259
18	19			1	1309
19	20			1	1334
20	21			1	1347
21	22			1	1371

ing the widest possible range of TL at a given time of the year, the data for June and July 1985 were pooled. Von Bertalanffy growth parameters were obtained as follows: females, k = 0.2 and L_∞ = 157 cm (Rn = 612); and males, k = 0.2 and L_∞ = 157 cm (Rn = 429).

Discussion

The area of greatest uncertainty for interpreting and measuring growth zones in shark centra is near the margin (Casey et al. 1985). Distinguishing the presence of the last ring is a common problem (Casey et al. 1985, Stevens 1975, Walker 1986). Using microradiography, the margin can be easily observed in school shark

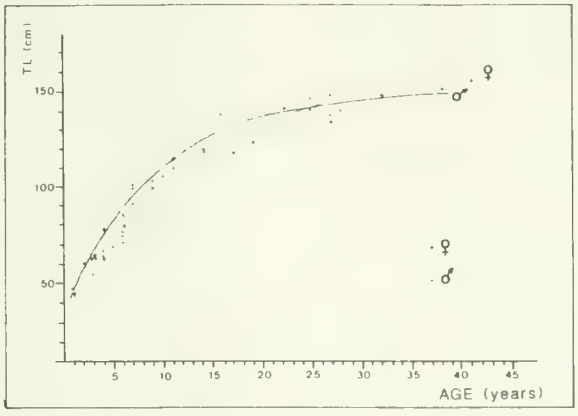

Figure 20
Von Bertalanffy growth curves for male and female *Galeorhinus galeus* and observed lengths-at-age.

vertebrae and the ring formation identified. This technique is not subject to problems derived from the presence of marginal connective tissue (Stevens 1975), and a large number of thin rings near the margin can be counted.

From observation of margins of vertebrae, we can conclude that ring formation probably occurred during the period June–September. The high percentages of ring formation observed in the sample indicated that the process probably extends over a larger period than observed in the current study, covering perhaps half of the year. The growth band would be formed during the remaining period, and the rings would thus be annual marks. However, as vertebrae were examined only for four-month periods (June–September), the need for a proper validation remains, as emphasized by Beamish and McFarlane (1983). The hypothesis that two rings could be formed during a year was disregarded, due mainly to the results of Grant et al. (1979). These authors estimated a longevity of 40 years for *Galeorhinus australis* (=*Galeorhinus galeus*, Compagno 1984) in South Australia, from mark-recapture data. Several individuals were recaptured after periods of more than 25 years at large, and 10% of the recaptures occurred 15 years after release. This evidence supported the hypothesis of one ring per year, which also led to the conclusion that individuals can attain up to 40 years of age.

Casey et al. (1985), observing a large number of rings near the margin, suggested that if these could be interpreted as annual marks, the ages determined for several species of sharks may have been underestimated. The present results agree with this hypothesis, and provide evidence that the school shark is a long-lived, slow-growing species.

The conclusion that the rings are translucent and strongly calcified, while the growth bands are optically opaque and less calcified is in agreement with the fact that the rings are stained dark by the silver nitrate technique (Stevens 1975, Cailliet et al. 1983). Casselman (1974, 1983) concluded that the translucent zone in calcified tissue of fish is more heavily mineralized than adjacent opaque zones and that calcium content is directly related to translucency.

In reference to the mode of calcification of cartilage, Moss (1977) wrote that "something radically different occurs in shark cartilage, making it certain that there can be no unitary description of vertebrate cartilaginous calcification." Hoenig and Walsh (1982) described the occurrence of vascularized cartilage canals in calcified vertebrae of several species of sharks. Many canals were found to contain blood cells, and they suggested a nutritive role for these canals. However, diffusion through the matrix is impossible after mineralization and in mammals; for instance, calcification of endochondral bone causes cellular degeneration and death of chondrocytes, because the isolated cells cannot maintain a normal metabolism (Robbins 1975). In the school shark, however, chondrocytes remain alive after calcification, as is evident from their normal, lipid-free appearance in calcified zones. Interchange between cells and vascular elements is probably sustained after mineralization by the canaliculi that were observed permeating the intercellular matrix.

The growth of crystals within a preformed organic structure is the basic mode of skeletal formation (Weiner 1984). Narrow uncalcified matrix areas observed at the edge of school shark vertebrae show that development of hyaline cartilage precedes the process of calcification. In addition, evidence of interstitial growth indicates that the tissue still remains uncalcified for a while after the appositional growth. In the vertebrae of embryos only the cone area was calcified. Among juveniles some uncalcified zones occurred also in the intermedialia. During the adult phase, the cone and intermedialia display the same mineralization pattern, with corresponding opaque and translucent alternate zones. This is evidence that the calcification, even when occurring at different times, follows the same pre-established rules. Weiner (1984) suggests that the organic matrix performs active, specific roles in this process. Growth of hydroxyapatite crystallites occurs in the space between collagen fibrils and perhaps within them (Glimcher *in* Kemp 1984). Therefore, regions of organic matrix formed during slow-growth phases would offer more space for crystal growth when exposed to the calcium and phosphate ions which form the mineral crystallites. Such regions, e.g., the rings,

would be characterized by relatively heavier calcification compared with the more rapidly growing, less calcified zones. In addition, the formation of the ring takes at least 4 months, but during the first 10 years of life the width of a ring is much less, in comparison with adjacent growth bands, than it would be if the growth rate were constant throughout the year. It is concluded that in *G. galeus* the ring represents a period of slow growth, and that mineralization is more intense during this period.

Vooren and Betito (In press) have shown that individuals of *Galeorhinus galeus* migrate northwards into the study area starting in April, until their peak abundance in September. At this time the school shark is abundant on the shelf south of lat. 32°S and scarce or absent further north. After September, the fish migrate southward from the study area, are scarce there in November, and absent in January and February. At the onset of winter, a marked change in temperature preference occurs, with most fishes occurring at 18–20°C from April to June and at 11–15°C in August and September, although water masses of higher temperatures are available during the latter months. The present data show that gravid females arrive first, making up all the April and May catches. From June onwards, other groups (adult males, non-gravid adult females and juveniles of both sexes) migrate into the area. The whole population experiences the decrease in temperature from June to August (Vooren and Betito In press). Thus, the period of slow growth and ring formation in vertebral centra coincides with this change in temperature preference of the population at the onset of winter. Similar results have been reported for other species (Stevens 1975, Jones and Geen 1977), confirming the general view that ring formation is associated with low temperature and slow vertebral growth (Longhurst and Pauly 1987).

As for the process involved, Casselman (1974) has suggested that during slow-growth phases, the amount of protein available for appositional growth might be reduced although minerals would still be available. In the shark vertebra, slow growth is evidently associated with a reduced rate of deposition of matrix components, which include both collagen fibrils and polysaccharides. Digestion and depletion of the carbohydrate moiety of the matrix during the slow-growth phase would facilitate interaction between collagen fibrils and mineral ions, thus promoting calcification. Mugiya (1987) has shown that in fish otoliths both calcium uptake and protein synthesis vary in an endogenous process controlled by hormones. In the school shark vertebrae, a matrix less dense in protein formed during slow-growth phases could be the cue to a higher calcium uptake to fill the space available for mineralization. Jones and Geen (1974) related wider rings with warmer years in spines of *Squalus acanthias*, and this relationship may explain the variation in the width of the rings which is observed in vertebrae of adult female school sharks (Fig. 15). Gravid females which migrate into the study area during March to May show preference for higher temperatures, and it is possible that they remain in the warmer part of the species' temperature range during the winter. If so, their rings might grow faster than in fishes that remain at lower temperatures. The distribution of the different components of the population in the study area during the winter should be investigated in detail to test this hypothesis.

Reading vertebrae is the most important tool for age determination in many elasmobranchs. Length-frequency analysis is most suitable for fast-growing species because of the assumption that all fishes in the sample have the same age at the same length (Longhurst and Pauly 1987). In slow-growing, long-lived species, however, a given size class contains several different age groups (Gruber and Stout 1983). The Von Bertalanffy growth parameters estimated by ELEFAN software (Pauly and David 1981), using length-frequency data, overestimated the growth rate determined by vertebral readings. These values were approximately the same as those found by Olsen (1954) when analyzing length-frequency data for the Australian school shark. Later, Grant et al. (1979), using tag-recapture methods, estimated lower values of growth rates and concluded that length-frequency analysis was impracticable in this species.

Acknowledgments

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Abstract.– Eighteen species of chaetognaths were identified from shelf waters in the Middle Atlantic Bight. Species composition in the water column and the hyponeuston was nearly identical, but the percent frequencies of the more common cold-temperate species were generally lower in surface collections. Mean surface salinity, weighted for abundance of individual chaetognath species in the hyponeuston collections, varied from 32.6 and 32.8 ‰ for the coastal- and estuarine-inhabiting *Sagitta tenuis* and *Parasagitta elegans*, to 34.8 and 34.9 for the offshore *Pterosagitta draco* and *Krohnitta pacifica*. Weighted mean temperatures ranged from below 14°C for *Mesosagitta minima*, *P. elegans*, and *Serratosagitta tasmanica* to over 24°C for *K. pacifica*. Overall association among Middle Atlantic Bight chaetognaths, measured for the 15 most frequent species in 716 collections by variance ratio, was significantly positive. Association between pairs of species was therefore also largely positive, with the important exception of *Parasagitta elegans*. This species, with a unique regional niche in low salinities and temperatures, was negatively associated ($p<0.01$) with five warm-water species (*Krohnitta pacifica*, *Ferosagitta hispida*, *Sagitta tenuis*, *Sagitta helenae*, and *Flaccisagitta enflata*). Most species reached maximum abundance at the surface near midnight. Exceptions included *Sagitta helenae*, with daylight maxima, and *Krohnitta pacifica*, *Ferosagitta hispida* and *Serratosagitta serratodentata*, showing crepuscular increases in abundance.

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Chaetognatha from the Central and Southern Middle Atlantic Bight: Species Composition, Temperature-Salinity Relationships, and Interspecific Associations*

George C. Grant

Virginia Institute of Marine Science and School of Marine Science
The College of William and Mary, Gloucester Point, Virginia 23062

Recognition of several chaetognath species along the northeastern coast of the United States is quite recent. Until 1960, only eight species had been identified from shelf waters off the Middle Atlantic states, i.e., the Middle Atlantic Bight from Cape Cod to Cape Hatteras; these were included in Bigelow and Sears (1939): *Eukrohnia hamata*, *Parasagitta elegans*, *Flaccisagitta enflata*, *Serratosagitta serratodentata* (including the then undescribed *Serratosagitta tasmanica*), *Flaccisagitta hexaptera*, *Pseudosagitta maxima*, *Krohnitta subtilis*, and *Pterosagitta draco***. Deevey (1960), in a study of the Delaware Bay region, added *Ferosagitta hispida*, *Sagitta helenae*, and *Mesosagitta minima* to the list of recognized species. Since her material had been collected three decades earlier (1929–31), it appears that pre-1960 studies had simply failed to distinguish between grossly similar species. *Sagitta tenuis*, *Sagitta bipunctata*, and *Krohnitta pacifica* were added by Grant (1963a, b) to the list of shelf species, and Grant (1967) later confirmed that the endemic shelf population of "*S. serratodentata*" in this region was actually *S. tasmanica*. Grice and Hart (1962) found other species in slope waters southeast of Long Island, New York, including *Pseudosagitta lyra*, *Mesosagitta decipiens*, and *Solidosagitta planctonis*. Thus, at the close of the 1960s, some 15 species were known from the shelf and the presence of others in surface slope waters suggested their likely occurrence over the shelf as well.

This study of Middle Atlantic Bight chaetognaths is based on an intensive series of collections from the central and southern bight. Presented here are the species composition in hyponeuston and subsurface collections, temperature-salinity-plankton (T-S-P) diagrams for the more common surface species, measurements of interspecific associations among chaetognaths, and a summary of diel abundance in the hyponeuston.

Methods and materials

Chaetognath collections

A transect of six stations (C1-J1, Fig. 1) off southern New Jersey was sampled quarterly for two years, October 1975–August 1977. Two more northerly stations (A2, B5) and a southern transect of four stations (L1-L6) were added in the second survey year

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** Taxonomy in this paper generally follows the revisions of Tokioka (1965) and Kassatkina (1971), but removes *Pseudosagitta lyra* and *P. maxima* from the genus *Flaccisagitta* in agreement with species groupings of Alvariño (1963).

(Grant 1977a, 1979, 1988). Routine collections at each station included paired 60-cm bongo net samplers (202 and 505 μm mesh nets), towed from just below the surface to near, but safely off, the bottom, then back to the surface (so-called double oblique tows; 220 samples), and eight surface layer (upper 10 cm) collections obtained at 3-hour intervals over a 24-hour period (496 samples), using a 1-m wide hyponeuston net (505 μm mesh). Of the 716 collections (Table 1), only 1 bongo and 79 hyponeuston (mostly daytime) collections lacked chaetognaths.

Laboratory processing

Collections were divided into successively smaller aliquots for the more numerous taxa, using a sample-splitting device of proven design (Burrell et al. 1974). However, chaetognaths were generally obtained from whole or half samples, unless very abundant.

Data analysis

Collection data were sorted by species, stations, and collection methods. Analysis of the relationship of species abundance to hydrography was limited to hyponeuston collections because subsurface tows were oblique, often traversing multiple layers of different water types. Mean temperatures and salinities of capture in surface-layer collections were calculated for each common chaetognath species, weighting each observed temperature and salinity by the size of catch ($\log N + 1$), where N = total catch in a standard 20-minute hyponeuston net tow at 2.5 knots. Thus,

$$\bar{T} = \frac{t_1(\log n_1 + 1) + t_2(\log n_2 + 1) + \ldots + t_n(\log n_n + 1)}{(\log n_1 + 1) + (\log n_2 + 1) + \ldots + (\log n_n + 1)}$$

$$\bar{S} = \frac{s_1(\log n_1 + 1) + s_2(\log n_2 + 1) + \ldots + s_n(\log n_n + 1)}{(\log n_1 + 1) + (\log n_2 + 1) + \ldots + (\log n_n + 1)}$$

where t_i, s_i, and n_i are the surface temperature, surface salinity, and total catch in each positive collection, respectively.

Presence, absence, and joint occurrences of the 15 most frequent species from both bongo and hyponeuston collections were used in an analysis of association between and among species. As recommended by Ludwig and Reynolds (1988), the significance of association among all 15 species and 716 collections was first tested simultaneously using a variance ratio (VR) derived from a null association model (Schluter 1984). The expected value of VR under the null hypothesis of independence is 1. When VR>1, a positive association of species is indicated; VR<1 indicates a negative association. A test statistic W = (N)(VR) provides a test of significance for deviations from 1. If species are not associated there is a 90% probability that W lies between the chi-square limits:

$$\chi^2_{0.05,N} < W < \chi^2_{0.95,N}.$$

Because of the large degrees of freedom in this study (where N = 716), critical values of χ^2 were approximated (see Zar 1984, p. 482).

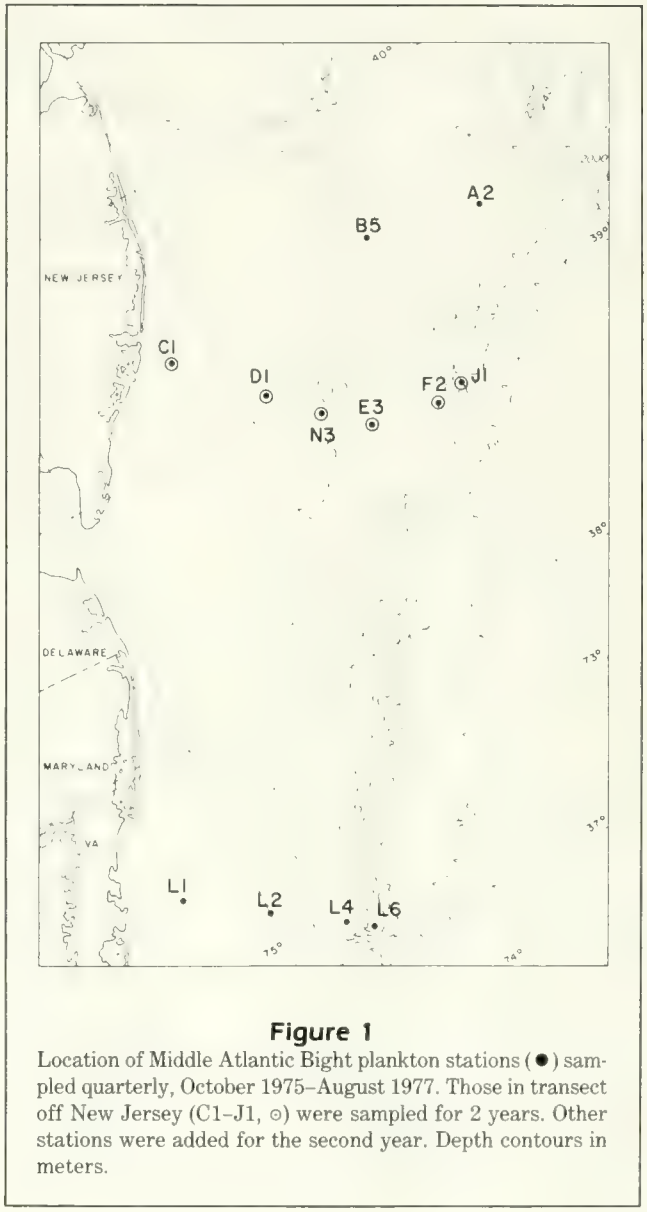

Figure 1

Location of Middle Atlantic Bight plankton stations (●) sampled quarterly, October 1975–August 1977. Those in transect off New Jersey (C1–J1, ⊙) were sampled for 2 years. Other stations were added for the second year. Depth contours in meters.

Relative strength of the association between pairs of species was measured using 2×2 contingency tables and Hurlbert's (1969) coefficient of interspecific association (C_8), as corrected by Ratliff (1982) for errors resulting from lack of absolute association (Pielou 1977). Yates' correction of chi-squared calculations was applied for low expected frequencies (Bailey 1981).

Table 1
Number of zooplankton collections obtained during eight seasonal cruises in the Middle Atlantic Bight, 1975–77.

		Subsurface		Surface	
		60-cm bongo nets		1-m hyponeuston net	
Cruise	Dates	202 μm	505 μm	505 μm	Total
1	23–29 Oct 75	6	6	48	60
2	5–16 Feb 76	6	6	48	60
3	8–16 Jun 76	6	8	52	66
4	31 Aug–9 Sep 76	6	7	48	61
5	5–28 Nov 76	22	21	75	118
6	20 Feb–6 Mar 77	21	21	75	117
7	17–28 May 77	21	21	75	117
8	19–29 Aug 77	21	21	75	117
Total		109	111	496	716

Results

Species composition

Eighteen species (11 genera) of chaetognaths were identified, 17 in both surface hyponeuston and subsurface bongo net collections (Tables 2 and 3). Compositional differences in the two lists were limited to the rarest species: *Sagitta bipunctata* was found only in hyponeuston collections, while *Pseudosagitta maxima* was restricted to subsurface collections. After adjustment for the 80 collections devoid of chaetognaths (79 surface and 1 subsurface collections), the percent frequencies of the most common cold-temperate species (*Serratosagitta tasmanica*, *Parasagitta elegans*, and *Mesosagitta minima*) were found to be much lower in surface collections. Warm-water chaetognaths (*Flaccisagitta enflata*, *Sagitta helenae*, *Pterosagitta draco*, *S. tenuis*, *Serratosagitta serratodentata*, *Ferosagitta hispida*, and *Krohnitta pacifica*) were either equally frequent in the two types of collections or more frequent in the hyponeuston.

Table 2
Percent frequency of chaetognath species occurrence in hyponeuston collections from eight quarterly cruises, 1975–77.

Cruise:	1	2	3	4	5	6	7	8	Total
Number of collections:	48	48	52	48	75	75	75	75	496
Serratosagitta tasmanica	50.0	43.8	48.1	33.3	66.7	61.3	17.3	21.3	42.5
Flaccisagitta enflata	18.8	—	1.9	81.2	77.3	34.7	24.0	73.3	41.9
Parasagitta elegans	35.4	85.4	92.3	14.6	6.7	16.0	58.7	14.7	37.3
Mesosagitta minima	2.1	22.9	—	—	50.7	30.7	2.7	9.3	16.5
Sagitta helenae	4.2	—	—	8.3	24.0	18.7	20.0	8.0	11.9
Ferosagitta hispida	—	—	—	35.4	21.3	—	1.3	14.7	9.1
Pterosagitta draco	2.1	8.3	—	16.7	8.0	17.3	6.7	—	7.5
Sagitta tenuis	—	—	—	31.2	20.0	—	1.3	2.7	6.7
Krohnitta pacifica	—	—	—	—	—	—	9.3	24.0	5.0
Serratosagitta serratodentata	—	—	—	4.2	4.0	6.7	2.7	8.0	3.6
Flaccisagitta hexaptera	—	10.4	—	10.4	2.7	6.7	—	—	3.4
Krohnitta subtilis	—	—	—	4.2	1.3	2.7	1.3	1.3	1.2
Mesosagitta decipiens	—	—	—	2.1	—	6.7	—	—	1.2
Pseudosagitta lyra	—	2.1	—	—	—	4.0	—	—	0.8
Eukrohnia hamata	—	2.1	—	—	—	2.7	—	—	0.6
Sagitta bipunctata	2.1	—	—	—	—	—	1.3	—	0.4
Solidosagitta planctonis	—	—	—	—	—	—	1.3	—	0.2

Temperature-salinity-abundance relationships

The chaetognaths were collected in a wide range of temperatures (2.2–26.6°C) and salinities 27.7–36.0‰ (Table 4). Weighted means of surface salinities measured at the time of hyponeuston collections were very similar among all common surface species, ranging from 32.6 and 32.8‰ for *Sagitta tenuis* and *Parasagitta elegans*, respectively, to 34.9‰ for *Krohnitta pacifica* (Table 4). Weighted mean temperatures, on the other hand, varied widely among species, from 12.9°C for *Mesosagitta minima* to 24.2°C for *K. pacifica*. Species occurring infrequently at the surface and excluded from Table 4 were those residing at greater depths, with surface occurrences mostly restricted to low winter temperatures. Relationships between surface abundance of common species and the two physical factors were further examined by plotting average daily catch (8 collections at 3-hour intervals) in standard hyponeuston collections, defined previously (Grant 1988) as 1-m neuston nets towed at 2.5 knots for 20 minutes; the sampler used typically fished the upper

10 cm of the sea surface so would more accurately be called a 'hyponeuston' net. Temperatures and salinities measured during collections containing chaetognaths were averaged at each positive station (Figs. 2 and 3).

Flaccisagitta enflata, *Sagitta tenuis*, *Ferosagitta hispida*, and, to a lesser extent, *S. helenae* and *Pterosagitta draco* were absent or uncommon in temperatures less than about 9°C (Figs. 2, 3), while few *Parasagitta elegans*, *Mesosagitta minima*, and *Pterosagitta draco* were found in warmest temperatures. *Serratosagitta tasmanica* was present in a very wide range of both temperature and salinity. Numbers of *Pterosagitta draco* were reduced in lower salinities as well as low temperatures; occurrences were in salinities higher than 34‰ except in the summer of 1976. *Sagitta helenae* and *Mesosagitta minima* were more frequent and numerous in higher salinities, while *S. tenuis* was absent from salinities greater than 35‰. Other species in Figures 2 and 3 were captured in various salinities.

Table 3

Percent frequency of chaetognath species occurrence in subsurface bongo collections from eight quarterly cruises, 1975–77.

Cruise:	1	2	3	4	5	6	7	8	Total
Number of collections:	12	12	14	13	43	42	42	42	220
Serratosagitta tasmanica	100.0	75.0	78.6	84.6	95.3	95.2	21.4	85.7	77.3
Parasagitta elegans	91.7	91.7	100.0	61.5	25.6	52.4	98.6	90.5	70.9
Flaccisagitta enflata	33.3	8.3	—	76.9	72.1	50.0	14.3	92.9	50.9
Mesosagitta minima	8.3	33.3	7.1	30.8	65.1	69.0	14.3	64.3	45.4
Sagitta helenae	—	—	—	—	18.6	26.2	14.3	9.5	13.2
Eukrohnia hamata	—	8.3	14.3	15.4	16.3	23.8	9.5	2.4	12.3
Flaccisagitta hexaptera	16.7	33.3	14.3	30.8	11.6	7.1	2.4	2.4	10.0
Pterosagitta draco	—	—	7.1	15.4	7.0	14.3	9.5	2.4	7.7
Sagitta tenuis	—	—	—	38.5	11.6	2.4	—	4.8	5.9
Serratosagitta serratodentata	—	—	—	—	2.3	2.4	4.8	16.7	5.0
Pseudosagitta lyra	—	8.3	—	—	4.7	7.1	7.1	2.4	4.5
Krohnitta subtilis	—	—	—	—	—	14.3	—	7.1	4.1
Ferosagitta hispida	—	—	—	23.1	7.0	—	—	4.8	3.6
Krohnitta pacifica	—	—	—	—	—	—	2.4	11.9	2.7
Mesosagitta decipiens	—	—	—	—	2.3	9.5	—	2.4	2.7
Solidosagitta planctonis	—	—	—	—	—	4.8	—	—	0.9
Pseudosagitta maxima	—	—	7.1	—	—	2.4	—	—	0.9

Table 4

Weighted means and ranges of temperature and salinity from surface collections at capture of the more frequent hyponeustonic chaetognaths, all cruises combined.

Species	Number of collections	Temperature (°C) $\bar{T}$	Temperature (°C) Range	Salinity (‰) $\bar{S}$	Salinity (‰) Range
Krohnitta pacifica	25	24.24	17.0–26.6	34.89	31.6–36.0
Serratosagitta serratodentata	18	21.25	8.1–26.6	34.57	31.7–35.9
Ferosagitta hispida	45	20.15	9.4–25.9	33.56	31.7–35.7
Flaccisagitta enflata	209	18.57	8.1–26.6	33.68	31.5–36.0
Sagitta helenae	58	16.76	6.3–26.6	34.38	31.7–36.0
Pterosagitta draco	37	15.87	8.1–22.3	34.75	32.4–35.9
Sagitta tenuis	33	15.83	9.1–24.6	32.59	31.7–34.8
Flaccisagitta hexaptera	17	14.00	8.4–22.3	34.56	33.1–35.8
Serratosagitta tasmanica	211	13.46	2.3–25.9	33.72	30.5–36.0
Parasagitta elegans	186	13.39	2.2–24.1	32.82	27.7–35.8
Mesosagitta minima	82	12.94	4.4–24.3	34.42	31.8–35.9

Interspecific association

Before examining association between pairs of species, the data were first tested for overall association using a matrix of the presence or absence of the 15 most common chaetognaths in 716 collections. Schluter's (1984) index of overall association (VR here, as in Ludwig and Reynolds 1988) for these 15 species was 2.108, indicative of a net positive association among the species. The null hypothesis of no association was rejected ($W = 1509$; 90% probability $654.9 < W < 779.3$).

Among paired-species associations, most statistically significant coefficients ($P < 0.05$) were positive (Table 5). Significant negative associations ($C_8 = -0.15$ to -0.73) were limited to six pairings of various species with *Parasagitta elegans* and the pair *Sagitta tenuis*–*Mesosagitta minima*. The sole significant positive association of *P. elegans* ($P < 0.05$) was with *Serratosagitta tasmanica*. Highest positive coefficients included associations among (1) the other most frequent chaetognaths, *Serratosagitta tasmanica*, *Mesosagitta minima*, and *Flaccisagitta enflata* ($C_8 = 0.18$ to 0.27); (2) deeper-living or outer shelf chaetognaths *Flaccisagitta hexaptera*, *Eukrohnia hamata*, *Pseudosagitta lyra*, *Mesosagitta decipiens*, and *Krohnitta subtilis* ($C_8 = 0.11$ to 0.30); and (3) the seasonal warm-water species *K. pacifica*, *Serratosagitta serratodentata*, *Ferosagitta hispida*, and *Sagitta tenuis* ($C_8 = 0.09$ to 0.26). *Sagitta helenae* and *Pterosagitta draco* shared positive associations with all three groups.

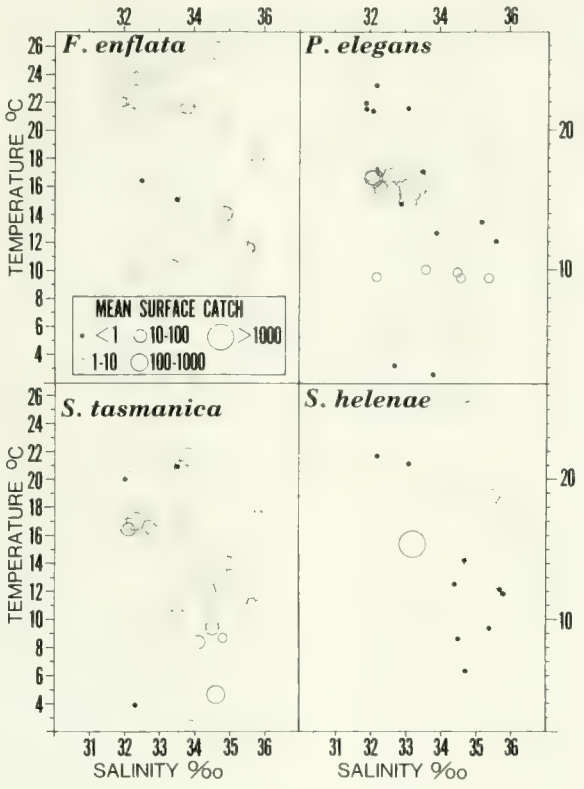

Figure 2

Temperature-salinity-abundance relationships of *Flaccisagitta enflata*, *Parasagitta elegans*, *Serratosagitta tasmanica*, and *Sagitta helenae* in the surface layer of the central and southern Bight. Each circle or dot represents the average catch for eight standard hyponeuston collections obtained over a 24-hour period at a single sampling location.

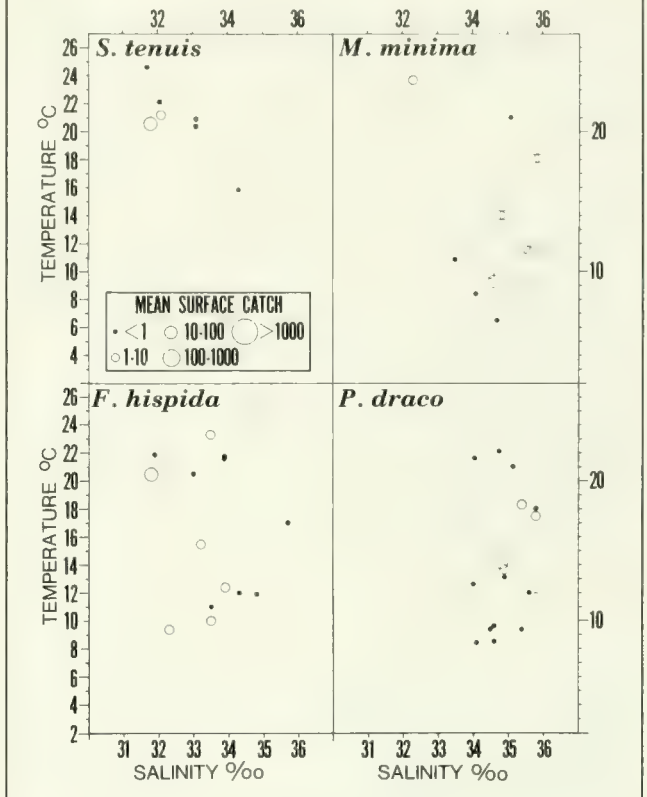

Figure 3

Temperature-salinity-abundance relationships of *Sagitta tenuis*, *Mesosagitta minima*, *Ferosagitta hispida*, and *Pterosagitta draco* in the surface layer of the central and southern Bight. See explanation in Figure 2 legend.

Diel distribution at the surface

Most of the chaetognaths commonly occurring in the surface layer reached peak densities near midnight (Table 6). *Flaccisagitta enflata*, *Krohnitta pacifica*, *Sagitta tenuis*, *Mesosagitta minima*, *Ferosagitta hispida*, and *Pterosagitta draco* all were caught in maximum numbers at that hour. Peak numbers of *Parasagitta elegans* and *Serratosagitta tasmanica* occurred somewhat earlier, but they were abundant throughout hours of darkness. There are also suggestions of dusk or dawn (or both) increases in abundance for *K. pacifica*, *F. hispida*, and *Serratosagitta serratodentata*.

Unlike any of the other chaetognaths, *Sagitta helenae* was decidedly more abundant at the surface in daylight hours, with 31.0 and 32.8% of total catches occurring around 1500 and 0900 hours, respectively.

Discussion

Eighteen species of chaetognaths are found in continental shelf waters of the Middle Atlantic Bight, including the 15 species on record after the 1960s plus the present records of three species previously known only from surface slope waters (Grice and Hart 1962). More recent studies of chaetognaths in this region have been restricted to estuaries (Grant 1977b, Sweatt 1980, Canino and Grant 1985) or to oceanic waters (Cheney 1985a,b). All of the western North Atlantic species labeled epipelagic or mesopelagic by Cheney (1985b) have been collected in shelf waters, so the present list appears reasonably complete. The composition of Middle Atlantic Bight chaetognath collections from hyponeuston and subsurface plankton tows was nearly identical. There were no frequent or abundant species unique to the hyponeuston, and all but the rarest species from subsurface shelf waters were taken at least occasionally from the surface layer. However,

Table 5

Number of occurrences (integers along the diagonal), coefficients of association (Hurlbert's C_R, right side of diagonal), and their statistical significance (** $P<0.01$ and * <0.05, respectively; blank = not significant, $P>0.05$, left side of diagonal) for chaetognaths collected during eight seasonal cruises in the Middle Atlantic Bight, 1975–77. Both subsurface and surface layer collections are included ($N = 716$); the three rarest species are excluded.

	pac	ser	his	ten	hel	dra	enf	min	tas	ele	ham	hex	lyr	dec	sub
Krohnitta pacifica	31	0.26	0.09	0	0.13	0.05	0.05	0	−0.09	−0.73	0	−1.00	0.04	0	0
Serratosagitta serratodentata	**	29	0.13	0	0.11	0.06	0.05	0.04	0.01	−0.19	0	0.04	0.05	0	0.05
Ferosagitta hispida	**	**	53	0.21	0	0.12	0.08	0.02	0.01	−0.64	−0.54	0.02	−1.00	0.02	0.03
Sagitta tenuis			**	46	0.09	0.07	0.08	−0.48	−0.18	−0.59	0	0	−1.00	0	0.02
Sagitta helenae	**	**		**	88	0.21	0.15	0.12	0.03	−0.40	0.06	−0.34	0.03	0.03	0.05
Pterosagitta draco		**	**		**	54	0.07	0.15	0.06	−0.22	0.13	0.09	0.05	0.08	0.09
Flaccisagitta enflata	**	**	**	**	**	**	322	0.22	0.18	−0.46	0.03	0.02	0.01	0.02	0.02
Mesosagitta minima		**		*	**	**	**	182	0.27	−0.15	0.08	0.08	0.05	0.03	0.04
Serratosagitta tasmanica		*			*	**	**	**	381	0.08	0.03	0.04	0.02	0.01	0.02
Parasagitta elegans	**		**	**	**		**	*	*	341	0.01	0	0	−0.27	0
Eukrohnia hamata					**	**	**	**	**		30	0.30	0.25	0.12	0.11
Flaccisagitta hexaptera						**		**	**		**	39	0.11	0.09	0.03
Pseudosagitta lyra		*				*	*	**	**		**	**	14	0.27	0.18
Mesosagitta decipiens						**	**	**	**		**	**	**	12	0.18
Krohnitta subtilis					**	**	**	**	**		**		**	**	15

Table 6

Diel distribution of the more common chaetognaths in hyponeuston collections. Data from 24-hour stations only, combined from eight seasonal cruises, 1975–1977.

	Hours (EST)								
	1200	1500	1800	2100	2400	0300	0600	0900	Total
	(% of total)								*N*
Flaccisagitta enflata	10.6	8.9	7.9	11.1	25.7	10.4	13.8	11.6	89,807
Parasagitta elegans	2.3	1.7	1.2	37.4	26.8	19.5	7.8	3.3	87,093
Serratosagitta tasmanica	1.3	1.3	6.7	30.3	27.9	23.5	6.2	2.8	16,283
Sagitta helenae	18.9	31.0	2.5	1.6	10.5	1.8	0.8	32.8	15,073
Krohnitta pacifica	3.5	10.3	11.8	2.5	34.0	1.9	23.0	13.1	2,573
Sagitta tenuis	0.5	0.9	10.3	13.7	45.2	18.2	7.9	3.3	2,283
Mesosagitta minima	0.9	1.4	2.4	8.9	60.4	13.6	7.5	4.9	1,383
Ferosagitta hispida	1.0	4.6	23.4	14.6	26.6	12.9	16.9	0	628
Serratosagitta serratodentata	0.2	2.9	28.2	8.3	0.7	3.4	56.2	0	411
Pterosagitta draco	0	0	1.7	11.9	32.2	27.1	26.3	0.8	118

there were apparent temperature-related differences in the percent frequency of chaetognath species in the two habitats. Cold-temperate species were less frequent at the surface than in the underlying water column, while warm-temperate or subtropical species were either equally frequent in the two habitats or more frequent in the hyponeuston.

The idea for T-S-P diagrams apparently originated with Pickford's (1946) study of the cephalopod *Vampyroteuthis*, and was first applied to chaetognaths by Bary (1959, 1963). T-S-P diagrams have since been used to relate abundance of chaetognaths to hydrography by numerous authors, including Sund (1961, 1964), Aurich (1971), Kotori (1976), Michel and Foyo (1976), O'Brien (1977), Nagasawa and Marumo (1982), and Andreu (1984). *Flaccisagitta enflata*, abundant in the Middle Atlantic Bight in warmer temperatures (averaging 18.6°C) and in various salinities (<32 to 36‰), occurred throughout the temperature and salinity ranges sampled by Nagasawa and Marumo (1982) and was apparently limited only by depth in the Caribbean (Michel and Foyo 1976). Sund (1961) also recorded *F. enflata* from 13–28°C and 32.6–35‰. T-S-P diagrams for *Parasagitta elegans* have been plotted by Bary (1963), who included the species in his "coastal (neritic) group," by O'Brien (1977) for populations to the west of Ireland, and by Kotori (1976) with ranges of temperature and salinity close to those in the present study. All agree in showing higher occurrence and abundance in colder water and an apparent tolerance for reduced salinity. Although the ranges of surface salinity in which Middle Atlantic Bight species were found were very similar, it is noteworthy that the five species with the lowest weighted means were the same five species recorded from within Chesapeake Bay (Grant 1977b) and in approximate inverse order of their estuarine abundance (*Sagitta tenuis*, $\bar{x}$ S = 32.6‰ and the most

abundant, to *Serratosagitta tasmanica*, $\bar{x}$ S = 33.7‰, the rarest in Chesapeake Bay). Aurich (1971) includes the only other known T-S-P diagram of *S. tasmanica*, used for a display of habitat differences with *S. serratodentata*. Michel and Foyo (1976) and Nagasawa and Marumo (1982) provided T-S-P diagrams for both *Mesosagitta minima* and *Pterosagitta draco*. Middle Atlantic Bight T-S-P diagrams agree with their depiction of greater abundance at higher salinities for these two species. Finally, Michel and Foyo's (1976) T-S-P diagram of *Ferosagitta hispida* shows a few occurrences at lower temperatures (13–17°C), but most at 27–28°C and in a broad range of salinities.

Association among the Middle Atlantic Bight species was generally positive, both in the multispecies case and between pairs of species. *Parasagitta elegans* provided an important and consistent exception, evidenced by its highly significant ($P<0.01$) negative associations with five warm-water species: *Krohnitta pacifica*, *Ferosagitta hispida*, *Sagitta tenuis*, *Flaccisagitta enflata*, and *Sagitta helenae*. Although both *P. elegans* and *S. tenuis* occur abundantly in coastal and estuarine waters in the Chesapeake region, they do so in opposite seasons, hence their negative association. The sole significant ($P<0.05$) positive association of *P. elegans* was with *Serratosagitta tasmanica*, and it appears to occupy a niche of low temperatures and salinities in this region, not unlike that of *Aidanosagitta crassa* in the East China Sea (Matsuzaki 1975). Highly significant positive associations were shared by (1) the endemic and abundant shelf species *Serratosagitta tasmanica*, *Mesosagitta minima*, and *Flaccisagitta enflata*, (2) the warm-water species *Krohnitta pacifica*, *Serratosagitta serratodentata*, *Ferosagitta hispida*, and *Sagitta tenuis*, and (3) the offshore, shelf-edge species *Flaccisagitta hexaptera*, *Eukrohnia hamata*, *Pseudosagitta lyra*, *Mesosagitta decipiens*, and *Krohnitta subtilis*. Three of the latter species comprised Matsuzaki's (1975) "Kuroshio water" species group.

Pearre (1973) determined that extensive diurnal migration takes place with *Parasagitta elegans*, perhaps related to feeding. Data in the present study on the diurnal distribution of the species in the hyponeuston also indicates a strong upward migration at night; numbers caught were about an order of magnitude higher at night than in daylight. Several other species showed similar sharp increases in abundance during darkness, including *Serratosagitta tasmanica*, *Krohnitta pacifica*, *Sagitta tenuis*, *Mesosagitta minima*, and *Pterosagitta draco*. Some were more abundant at dawn or dusk, or, in the case of *Flaccisagitta enflata* and *Sagitta helenae*, were present in considerable numbers in daylight. Among these species, Nagasawa and Marumo (1982) found evidence for diurnal migration in *F. enflata*, *P. draco*, and *K. subtilis*, none for *K. pacifica*, and mixed evidence for *M. minima* and *F. hexaptera*. However, in the present comparison of day and night hyponeuston collections, only a short migration would be required to populate and depopulate the surface layer diurnally. Such fine-scale diurnal movements likely do occur within the surface mixed layer, but are most difficult to measure.

Acknowledgments

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Abstract.–The trawl fishery for ocean pink shrimp (*Pandalus jordani* Rathbun) has increased dramatically since the early 1970s. Catch and effort statistics and catch sampling data from 1968-88 were analyzed to evaluate changes in the shrimp population structure. Carapace length at age one and two have increased significantly since 1978, concurrent with a reduction in fishery catch per unit effort, strongly indicating density-dependent growth. The seasonal pattern of growth provides further evidence for density-dependent growth. The number of age three shrimp in the catch has declined markedly since 1978, while age one shrimp have increased from 30.6% of the catch to 69.2%. The percentage of age one shrimp maturing as females has increased to 30-50% in some years, while the overall percentage of males shows no trend. The changes in growth, and age and sex composition of the catch are attributed in part to the impact of the trawl fishery, which is currently continuing to intensify. Density-dependent growth, and the ability to accelerate the sex change process make pink shrimp resistant to over-harvest. However, at some exploitation level the reduction of the age 1 spawning stock should begin to reduce subsequent recruitment. Recent strong year classes indicate that the fishery probably has not reached that level of exploitation.

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Fishery-induced Changes in the Population Structure of Pink Shrimp *Pandalus jordani*

Robert W. Hannah
Stephen A. Jones

Oregon Department of Fish and Wildlife, Marine Region
Marine Science Drive, Bldg. 3, Newport, Oregon 97365

The Pacific trawl fishery for pink shrimp *Pandalus jordani* Rathbun has developed from a fishery with landings of around 220 mt in the early 1960s to a fishery regularly landing in excess of 18,000 mt. In six of the thirteen years since 1975, combined landings for the states of California, Washington, and Oregon have exceeded 24,000 mt. Pink shrimp range from San Diego, California to Unalaska, Alaska (Butler 1964); however, the majority of the catch is taken between Cape Mendocino, California and Destruction Island, Washington. The development of the fishery has been well summarized by Dahlstrom (1970), Fox (1972), Zirges and Robinson (1980), and others.

Saelens and Zirges (1985) described the 1984 fishery for pink shrimp and suggested that there was some evidence of changes in the shrimp population structure that were possibly the result of fishing. They noted improved growth and higher levels of age-1 shrimp in the catch, relative to earlier years. Fishing effort and shrimp catch have continued to increase since 1984. Given the continued development of this fishery, we felt that some fishery-induced changes in the population structure would be evident in a thorough review of the fishery sampling data. We examined 23 years of information from the pink shrimp fishery off the coasts of Oregon and northern California to search for the classic population responses to increased fishing. Specifically, we looked for persistent shifts in age and sex composition, changes in the age of female maturity, evidence of reduced stock biomass, and improved shrimp growth as a response to lower biomass. As a final step, we attempted to relate the observed changes to the development of the fishery and alternatively to environmental factors.

Methods

We examined monthly sample data from the landed catch of pink shrimp for the years 1966–88. The data is comprised of several samples from each statistical area (Fig. 1) and month of the fishing season. The season currently runs from April through October, but has been longer in the past. Individual samples for each area and month (area–month) were combined for analysis of age and sex composition. Sample summaries provide individual carapace lengths and average weight expressed as the number of whole shrimp per pound. Shrimp are classified as male, female, or transitional based upon close examination of the inner ramus of the first pleopod (Tegelberg and Smith 1957). Shrimp age is determined by modes in the combined length-frequency histogram (Zirges et al. 1981). Nadirs in the histograms define the range of carapace lengths corresponding to each age group, then ages are assigned to individual shrimp.

Zirges et al. (1982) concluded that pink shrimp from statistical areas

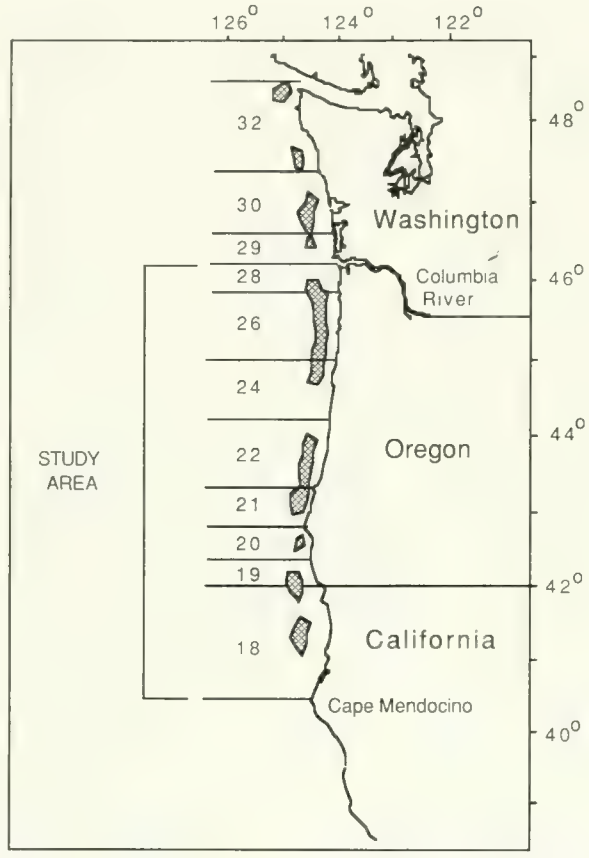

Figure 1
Location of commercial concentrations of pink shrimp *Pandalus jordani* along the U.S. Pacific coast (shaded areas) and statistical areas 18–32.

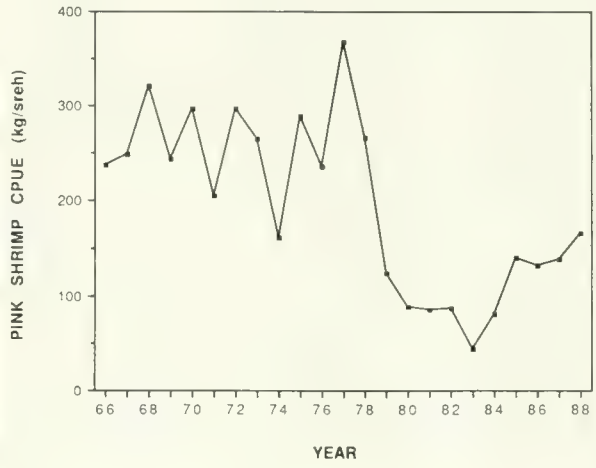

Figure 2
Catch-per-unit-effort (kg/single-rig equivalent hour) for the pink shrimp fishery in statistical areas 18–28 for the years 1966–88.

18–28 constituted a single stock, based upon an analysis of growth, maturation rates, and coastal oceanographic conditions. We used the same stock unit to allow us to draw upon the summarized sample data from Zirges et al. (1982) for the years 1966–81.

To evaluate the effect of shrimp density on growth, we compared shrimp carapace length at age for two time-periods representing different levels of population biomass. We use the term "density" in the sense of biomass per unit area rather than the number of individuals per unit area. We used catch-per-unit-effort (CPUE) as our index of shrimp density.

During the years 1975–78 major improvements in trawl design were implemented by the shrimp industry. Prior to 1976, the predominant shrimp net was a 57-foot (headrope) Gulf of Mexico style, Marinovitch trawl, with a 4-foot vertical opening (Zirges and Robinson 1980). During the years 1975–78 the majority of the fleet switched to locally produced 70–90 foot (headrope) box trawls. The new trawls have proven to be much more efficient for pink shrimp. Besides being generally bigger, they open to a height of 12–18 feet, improving fishing for pink shrimp, which come up off the bottom under reduced light conditions. Increased cloud cover and time of day were shown to bring concentrations of shrimp up off the bottom at least 8 feet (Beardsley 1973). The Oregon box trawls are also constructed differently from the Marinovitch trawls. They are much longer, employ a slower taper, and are hung with considerable "slack" webbing, all contributing to a much more efficient trawl for pink shrimp. The effort data series is not corrected for these gear improvements. Therefore, CPUE data understate the magnitude of biomass reduction since 1978 (Fig. 2). Accordingly, we tested growth for the two time-periods, 1966–78 and 1979–88. We considered these periods to be representative of the virgin stock biomass and the reduced biomass, respectively. We used F-tests to identify significant differences in length at age.

Four area–months were selected as indices for analysis of age-1 and -2 shrimp growth, based upon the completeness of the time-series data. For age-1 shrimp, the months of April–June were excluded because in some years age-1 shrimp are not fully recruited to the trawl gear in those months. For age-2 shrimp, the months of September and October were excluded because in recent years age-2 and older shrimp comprise a small percentage of late-season catches. Given these criteria, the index area–months selected for age-1 shrimp were

Area 22–August, Area 21–July, Area 26–August, and Area 19–August. The most complete time-series for age-2 shrimp were found to be Area 19–August, Area 22–April, Area 21–June, and Area 26–May. Age-2 length comparisons are not independent of the age-1 results. The age-2 analysis was employed to help rule out any apparent changes in growth of age-1 shrimp caused by changes in fishery or gear selectivity over time.

Table 1

Comparison of mean carapace length for age-1 and -2 pink shrimp for the years 1966–78 and 1979–88 (single classification ANOVA with unequal sample sizes).

Area–Month	Years	Mean carapace length (mm)	*N* (years)	*F* value	*P>F*
Age 1					
Area 22–August	1966–78	16.04	13	23.40	0.0001
	1979–88	17.32	7		
Area 21–July	1966–78	15.65	9	6.11	0.0251
	1979–88	16.44	9		
Area 26–August	1966–78	15.56	9	14.09	0.0021
	1979–88	16.67	7		
Area 19–August	1966–78	16.44	8	27.07	0.0002
	1979–88	17.79	7		
Age 2					
Area 19–August	1966–78	19.98	8	76.43	0.0001
	1979–88	21.84	7		
Area 22–April	1966–78	18.03	13	26.70	0.0001
	1979–88	19.59	9		
Area 21–June	1966–78	19.01	8	37.57	0.0001
	1979–88	20.60	9		
Area 26–May	1966–78	18.75	11	7.98	0.0112
	1979–88	19.69	9		

To further investigate factors influencing age-1 shrimp growth, we conducted some exploratory correlation analysis. Since the time-series for the most complete index areas still contained some missing samples, and since many of the environmental factors we wished to test are not area-specific, it was desirable to combine our four age-1 growth indices into one, more complete, time-series. Carapace length at age in pink shrimp exhibits a gradient effect increasing from north to south along the coast and also increasing through the season. To remove these effects and yet preserve the interannual variations in size, one of the four indices was chosen as a standard and the other three were adjusted by an additive factor equal to the difference between the mean of the chosen standard and that of the individual index area–month. Subsequently, the adjusted index area–months were averaged into one time-series. Area 22 was chosen as the standard, and the resultant time-series for age-1 was without gaps and most points were based on two or more adjusted means.

Linear regression was used to examine factors influencing variation in this age-1 shrimp growth index. The independent variables tested included sea surface temperature at Charleston, Oregon (Oreg. Dep. Fish. Wildl., unpubl. data) upwelling at 45°N, 125°W (Bakun 1973; NMFS Pacific Environ. Group, Monterey, CA, unpubl. data), inverse-barometer corrected sea level at Newport, Oregon, (Pittock et al. 1982; Pittock, unpubl. data), and catch per unit effort in the fishery as an index of shrimp density. Kruse (1981) found inverse barometer-corrected sea level at Newport and Neah Bay to be highly correlated with sea-bottom shelf temperatures near Newport. We tested each variable with no time lag (year t) and a 1-year time lag (t – 1) to match growth in an earlier life stage. Adjusted sea level at Newport was tested both with and without the 1983 data point, a year of abnormally high sea level caused by a strong El Niño event. Finally, we tested the average CPUE for the years t and t – 1 combined, to represent the average density encountered over the life of an age-1 shrimp. Second-order polynomial regression was also used to test each variable for a significantly curvilinear relationship with the age-1 growth index (Ricker 1975).

Correlation analysis with time-series data of short duration is often of limited value, but does help to generate initial hypotheses to be tested with the accumulation of future data (Ricker 1975). Short time-series often exhibit unidirectional time trends causing spurious correlations. For these reasons, we felt that correlation analysis would be a relatively poor tool for differentiating the relative importance of the various factors to shrimp growth, but would help to identify the factors which deserve future analysis. Consequently, correlation analysis was not pursued further in this study.

For analysis of trends in the sex composition data, we once again relied upon four index–area months with the most complete time-series. The four index–areas employed were Areas 19 and 28 in October and Areas 21 and 22 in September. Pink shrimp are protandrous hermaphrodites and mate primarily in September and October each year (Pacific Fisheries Management Council 1981). They usually mature first as males in the fall at about 1½ years of age, and after spawning

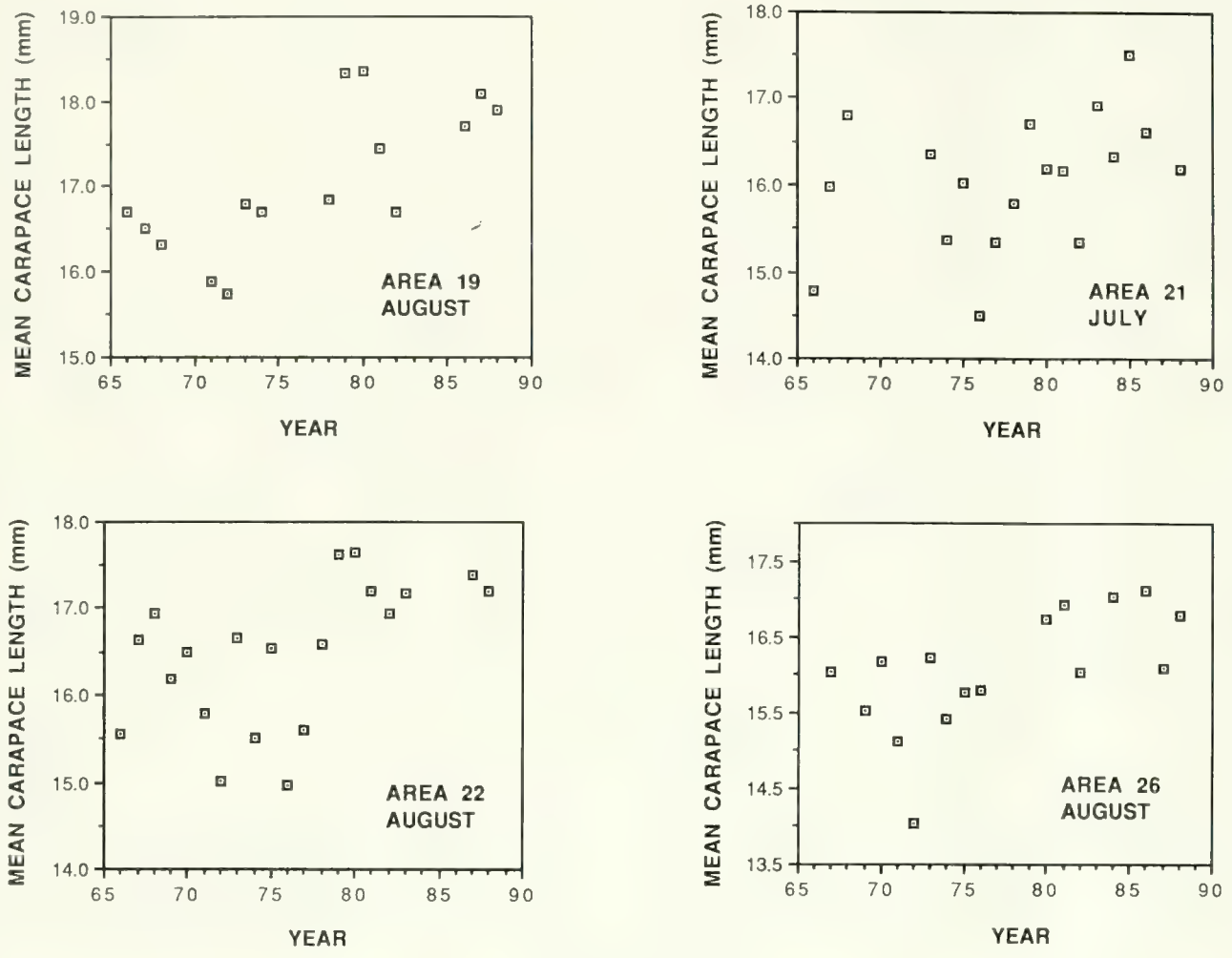

Figure 3
Mean carapace length of age-1 pink shrimp from 1966–88 for the selected index area–months.

go through a transitional phase, usually maturing as a female the following year at age 2½. Age-1 shrimp that mature directly into females, bypassing the male phase, are called primary females. We examined the data for trends in the percentage of primary females and the overall percentage of male shrimp.

Results

We found significantly improved growth of pink shrimp for the 1979–88 period as compared with the 1966–78 period. Mean carapace lengths for all four age-1 index area–months were significantly greater in 1979–88 (Table 1, Fig. 3) based on two-tailed F-tests. Mean carapace lengths were also greater for the four age-2 index area–months (Table 1, Fig. 4). Since age-2 shrimp are fully recruited to the trawl gear, this result rules out any apparent increase in mean length due to fishery or gear selectivity or accelerated sex change of age-1 shrimp. The time-series of catch per unit effort (Fig. 2) indicates that the population biomass has been reduced since 1978.

The increase in growth demonstrated for the 1979–88 catch years represents a substantial increase in average weight. Using the age-1 composite growth index, the mean carapace length of age-1 shrimp has increased from 16.1 to 17.4mm. From the length-weight relationship developed by Zirges et al. (1982);

$$\ln W = -7.94746 + 3.2097 \ln L,$$

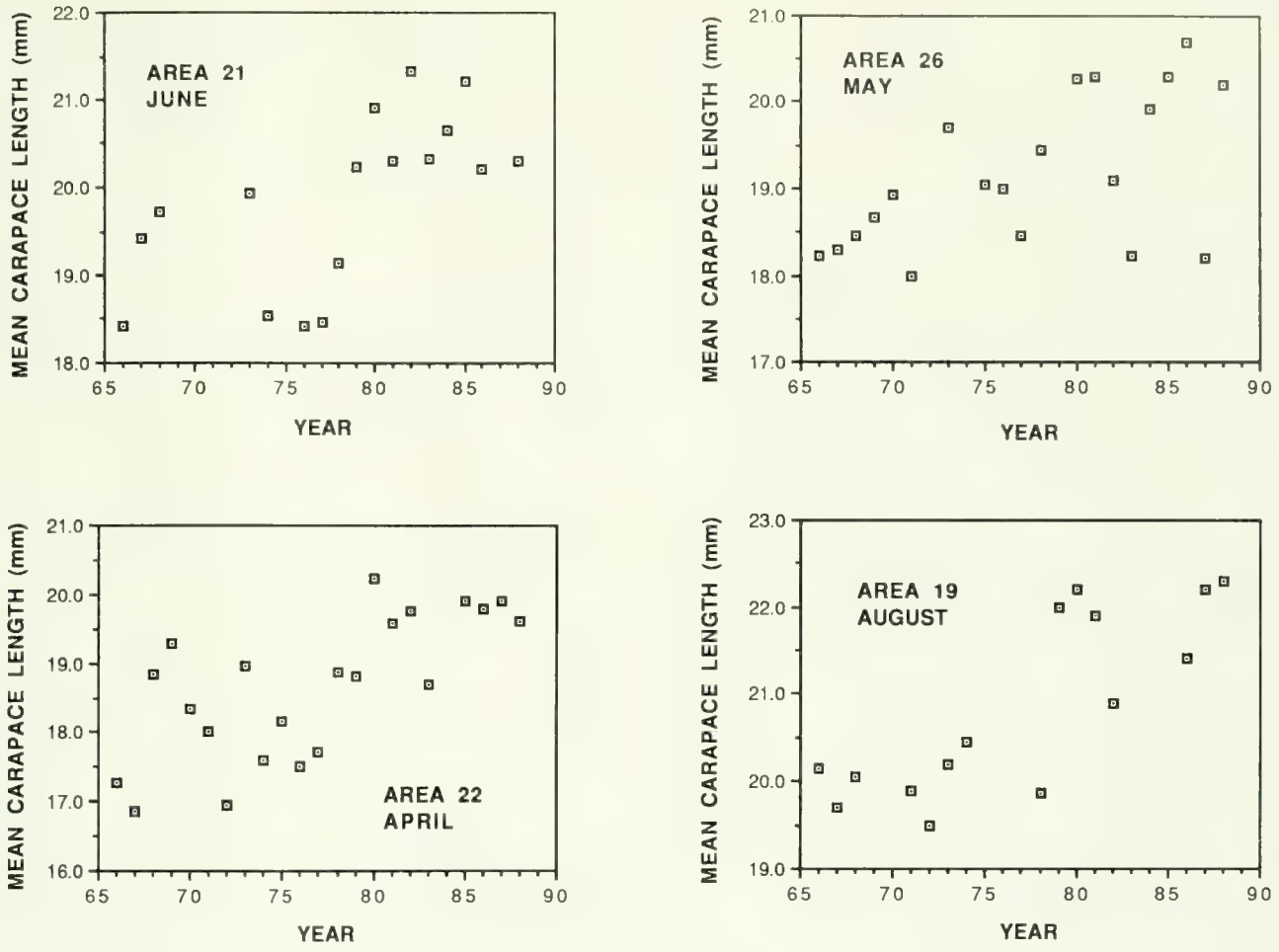

Figure 4
Mean carapace length of age-2 pink shrimp from 1966–88 for the four index area–months.

where W = Weight (g), and
L = Length (mm),

this represents a 28.4% increase in mean weight at age. This is an approximate figure scaled for Area 22 data; however, other areas yield similar results.

The exploratory correlation analysis (Table 2) shows that sea surface temperature at Charleston, Oregon, and sea level at Newport, Oregon (Fig. 5), are positively correlated with the age-1 growth index. However, CPUE (Fig. 6) is negatively correlated with the age-1 growth index suggesting density-dependent growth.

Adjusted sea level at Newport and sea surface temperature at Charleston displayed evidence of a curvilinear relationship, of decreasing slope, with the age-1 growth index. However, the regression coefficients of the second-order polynomial regressions were only significantly different from zero (t-test, $P>0.05$) for adjusted sea level in year t – 1. The curvature of this relationship is strongly influenced by a single outlier, the 1983 sea level, data point. With this point deleted, the coefficients of the polynomial regression are not significantly different from zero, while the adjusted r-squared value for the simple linear regression increases to 0.528 (Table 2). This suggests that bottom temperature is also influencing shrimp growth.

Graphs of mean length at age for areas 19, 21, 22 and 26 (Fig. 7) show that much of the difference in growth between the 1965–76 and 1977–86 broods is already apparent at age-13 months when the fishery first catches age-1 shrimp. This is not surprising, since density-dependent growth has been demonstrated more frequently for species during the immature phase, with density-dependent changes in fecundity more prevalent in the adult phase (Bailey and Almatar 1989). With the exception of area 19, the curves for the

1965–76 broods show some tendency for the rate of increase in length to slow in the fall, near the end of the fishing season, at ages 17–19 and 27–30 months. The curves for the 1977–86 broods differ somewhat in that this slowing of growth in the fall is less pronounced. These data suggest that density-dependent growth in pink shrimp may continue into the adult stage.

The impact that the trawl fishery has had upon the shrimp population is very evident from an examination of age composition of the catch (Fig. 8). In catch years 1966–78, age-3 shrimp comprised an average 20.4% of the catch by number, falling to an average 4.9% for the years 1979–88. Conversely, age-1 shrimp have risen from an average 30.6% in the early period to 69.2% of the catch in recent years. The increases in relative abundance of age-1 shrimp may be explained in part by the fact that they are recruited to the trawl gear earlier in the season due to increased size at age in recent years. The decline in absolute numbers of age-3 shrimp (Fig. 8) cannot be explained by changes in gear selection. The observed changes in age structure of the catch must be at least partly due to the impact of the trawl fishery.

The change in age composition of the catch is also reflected in the mean size of shrimp in the landed catch. The average number of shrimp per pound increased from 109.4 during the 1966–78 period to 118.9 for the 1979–88 period. The decline in numbers of older shrimp has been accompanied by an increase in the percentage of shrimp maturing directly into females at age-1 (Fig. 9). In recent years, levels of primary females as high as 30–50% are common. This effect has compensated for the higher cumulative harvest rates on age-2 and

Table 2

Results of exploratory regression analysis of potential factors influencing carapace length of age-1 pink shrimp. The dependent variable is an index of age-1 shrimp growth based upon mean carapace length from four selected statistical area–months.

Model	Independent variables*	Intercept	Coefficient	Adjusted r^2	P
1	U_t	—	—	—	NS
2	U_{t-1}	—	—	—	NS
3	SL_t	—	—	—	NS
4	SST_t	12.474	0.426	0.191	0.0307
5	SST_{t-1}	12.587	0.419	0.198	0.0323
6	SL_{t-1}	−20.096	0.125	0.348	0.0075
8	$CPUE_t$	17.709	−0.005	0.349	0.0018
7	$CPUE_{t-1}$	17.649	−0.005	0.287	0.006
9	Mean $CPUE_{t,t-1}$	17.877	−0.006	0.391	0.0009
10	SL_{t-1}**	−46.171	0.214	0.528	0.0009

*U = April–October upwelling from 45°N lat. 125°W long.
SL = Mean annual inverse-barometer corrected sea level at Newport, OR
SST = January–February mean sea surface temperature at Charleston, OR
CPUE = Catch-per-unit-effort for the pink shrimp fishery in statistical areas 18–28.
t = Calendar year of growth index.
** 1983 sea level deleted.

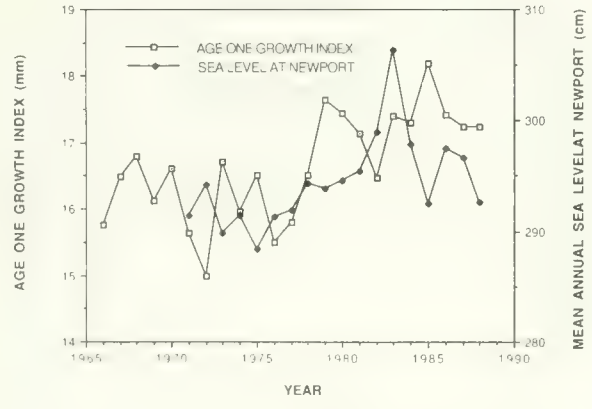

Figure 5

Age-1 growth index (mm) and mean inverse-barometer corrected sea level (cm) at Newport, Oregon for the years 1966–88 and 1971–88, respectively.

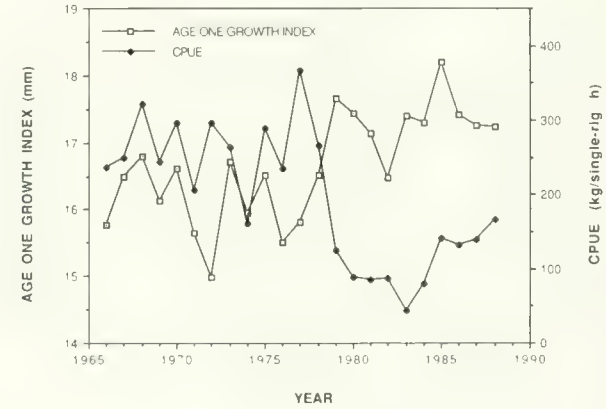

Figure 6

Age-1 growth index (mm) and pink shrimp catch-per-unit-effort (kg/single-rig equivalent hour) for 1966–88.

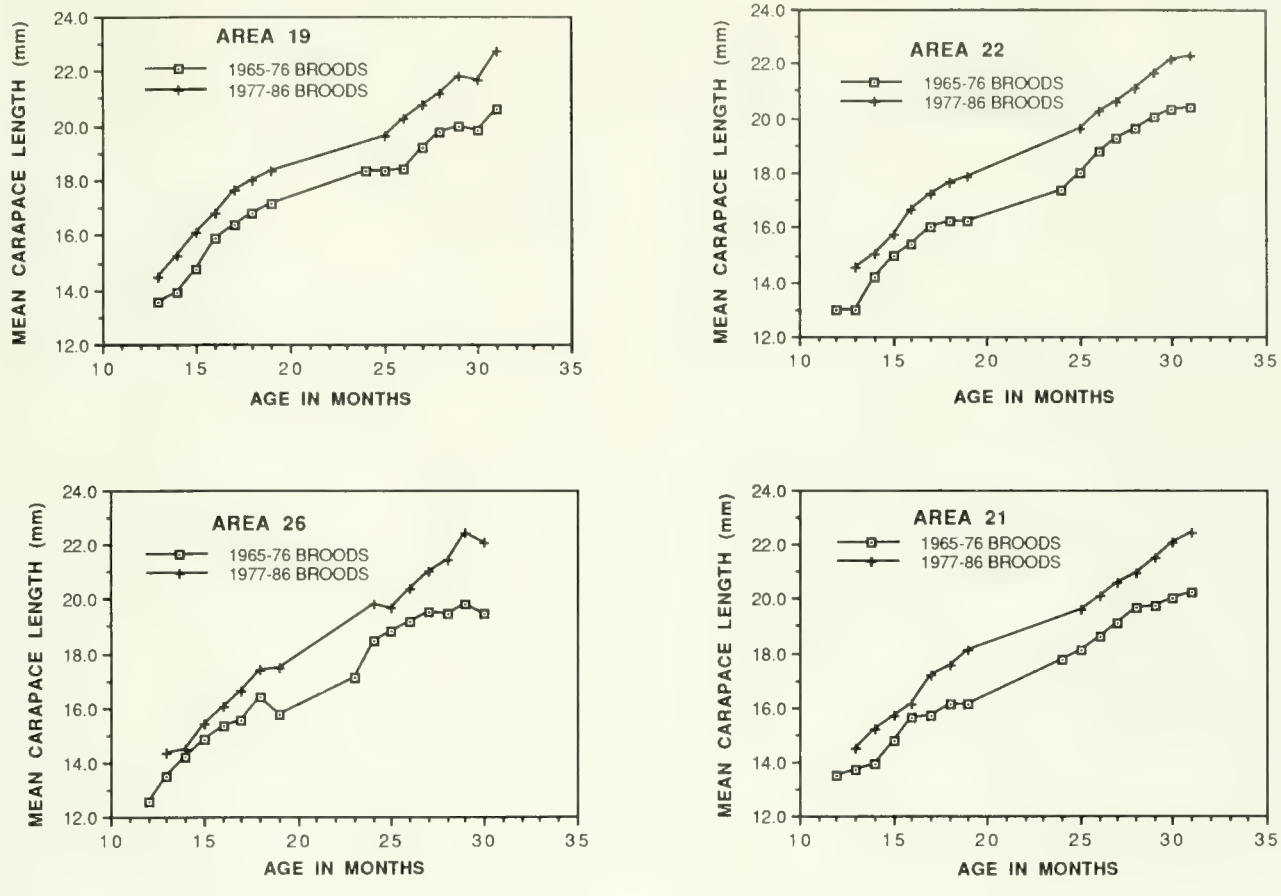

Figure 7

Mean length at age for the 1965–76 and 1977–86 broods of pink shrimp from Oregon statistical areas 19, 21, 22, and 26.

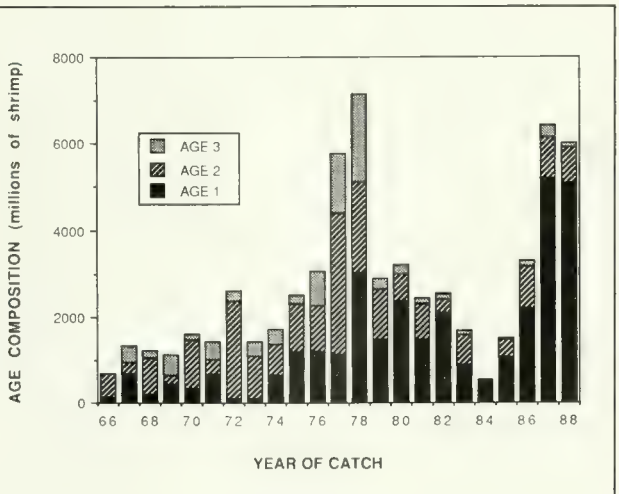

Figure 8

Age composition by number of the catch of pink shrimp from statistical areas 18–28 for the years 1966–88.

older shrimp, and a sexually balanced breeding population has been maintained (Fig. 10).

Discussion

Our analysis supports a conclusion that pink shrimp are exhibiting density-dependent growth. The transition to larger mean size at age between 1978 and 1979 coincides nearly exactly with the large drop in fishery CPUE, and the shift in age composition of the catch toward younger ages (Figs. 6, 8). This is probably due to the intensive development of the fishery during the mid 1970s (Fig. 11). The fishery continued to intensify after 1978, with subsequent effort levels falling to pre-1977 levels only in the years 1983–1985 (Fig. 12). The persistence of reduced CPUE and reduced mean age at capture are classic results of an intense size-selective harvest causing reduced levels of population biomass.

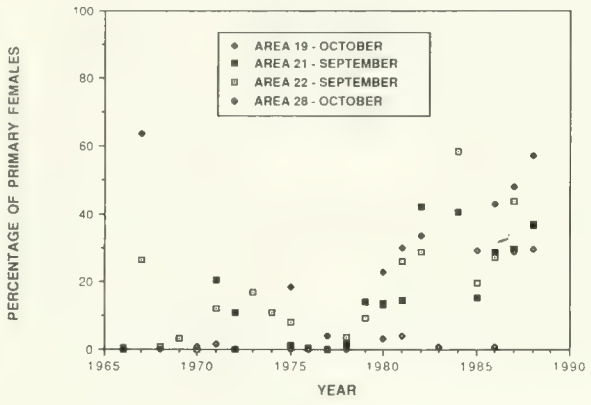

Figure 9
Percentage of age-1 pink shrimp maturing as females for four index area–months for the years 1966–88.

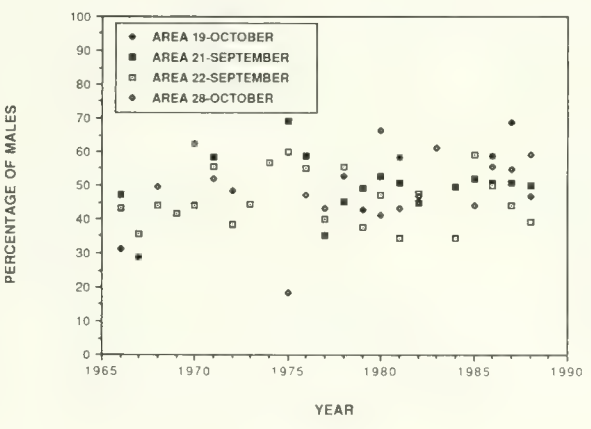

Figure 10
Percentage of male pink shrimp for four index area–months for the years 1966–88.

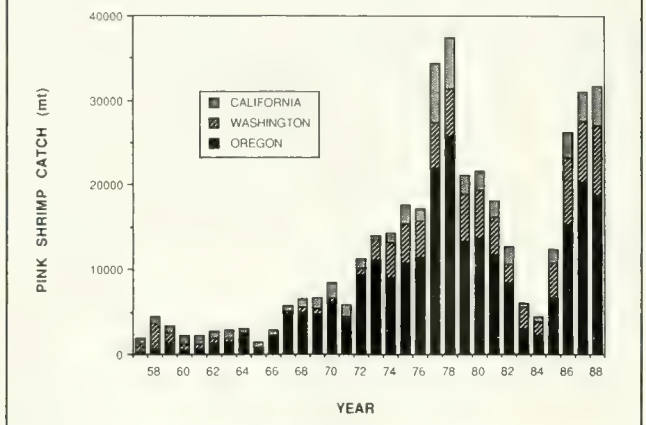

Figure 11
Combined landings of pink shrimp for the states of California, Oregon, and Washington for the years 1957–88.

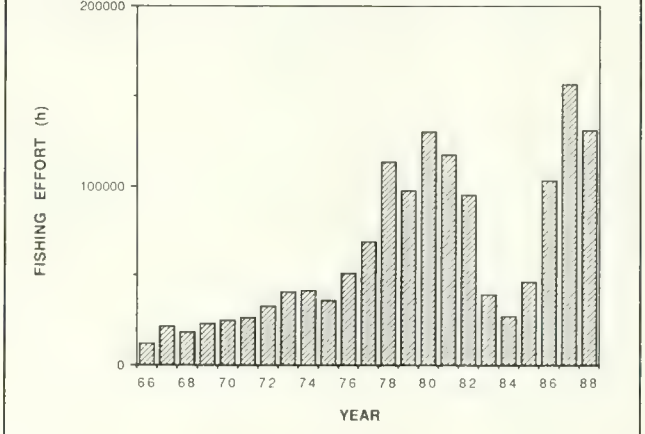

Figure 12
Fishing effort (single-rig equivalent hours) for pink shrimp in statistical areas 18–28 for the years 1966–88.

The pattern of growth in the index areas (Fig. 7) shows a slight tendency toward improved late-season growth in recent years, coincident with the season of minimum shrimp density on the grounds (Fig. 13). During the fall, age-0 shrimp begin to appear in the trawl catch in small numbers (Zirges et al. 1982). These data suggest that the improved growth occurring prior to age-13 months may be a result of decreased shrimp densities created by the trawl fishery.

The time-series of CPUE probably understates the true drop in shrimp biomass since 1978 due to the gear improvements mentioned previously. The difference in mean size at age demonstrated after 1979 may also be understated by the data shown in Figure 9. Prior to 1969 the minimum codend mesh allowed in the Oregon pink shrimp fishery was 38mm (including one knot), while from 1969 onward codend mesh size has been unregulated (J.T. Golden, ODFW, Newport, 1981 draft). The lower curves in Figure 7, therefore, probably overestimate the mean size at age-1. Since 1979, with larger mean size, age-1 shrimp have been more completely sampled by the gear. D.R. Bernard (Oregon State Univ., Corvallis, 1983 draft) estimated that pink shrimp were fully recruited to the 38mm mesh trawl

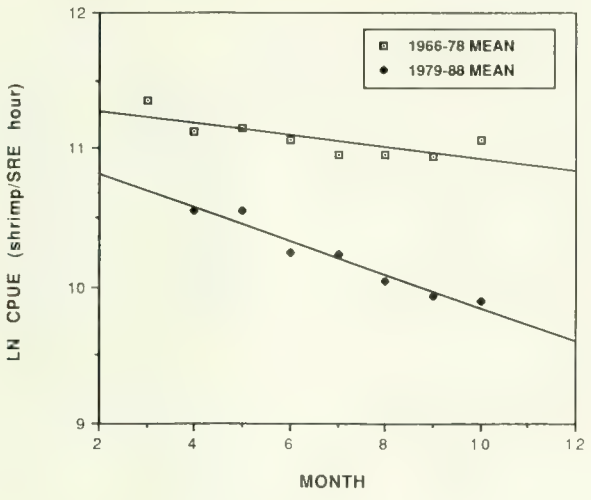

Figure 13
Log of mean catch-per-unit-effort (shrimp/single-rig equivalent hour) by month for 1966–78 and 1979–88.

at 16.6mm carapace length. Since 1979, age-1 shrimp are fully recruited to a 38mm trawl in the later months of the season and to smaller gear even sooner. In earlier years, samples were biased toward only larger age-1 shrimp, and thus, by comparison, understate the increase in growth observed since 1979.

Our exploratory correlation analysis is inconclusive in differentiating between density-dependent and environmental factors as influences on shrimp growth. While the underlying relationship between the age-1 growth index and the environmental variables tested is most likely curvilinear (Ricker 1975), the relatively narrow range of environmental variability being tested in this case warranted the simple linear approximation. The combined age-1 growth index was closely correlated with our index of shrimp density, CPUE, despite the fact that CPUE is a relatively poor index of density. We showed CPUE to be negatively correlated with mean size at age over rather large changes in CPUE. Of course, smaller changes in CPUE, not associated with major changes in population density, should be positively correlated with growth, causing CPUE to be a poor index of shrimp density. We also found adjusted sea level at Newport, Oregon in year $t-1$ to be closely correlated with the age-1 growth index, indicating that warmer bottom temperatures may have caused improved shrimp growth after 1978. Rothlisberg (1975) showed shrimp growth to be positively correlated with temperature under laboratory conditions. It is possible that elevated sea levels improve growth over the normal range observed, but at extreme levels such as occurred in 1983, the virtual complete shutdown of coastal upwelling has the reverse effect (Pearcy et al. 1985, Miller et al. 1985).

The hypothesis that sea surface or bottom temperatures (as inferred from sea level data) are controlling shrimp growth will most likely be tested over the next decade or two. In time, the relatively warm ocean conditions experienced off the Oregon coast since 1978 will probably be replaced by a colder, upwelling-dominated regime, similar to the early 1970s. The mean increase in length we have measured is equivalent to a 28% increase in average weight at age. If sea-bottom temperatures are controlling growth and return to lower levels, the drop in fishery yield will be profound. Conversely, it is unlikely that the shrimp fishery will be substantially reduced, allowing standing stocks of shrimp to rebuild to near virgin levels of the early 1970s. Thus, as we see the subsequent trend in mean carapace length at age of pink shrimp, our hypothesis of density-dependent growth will be tested further.

Charnov et al. (1981) showed that reductions in the population of age-2 and older shrimp (predominantly female) should result in increases in primary females. If Charnov is correct, the trawl fishery, through selective removal of older shrimp, should be causing this effect in the population. The result of accelerated sex change should be higher levels of primary females and a roughly stable sex ratio. Jensen (1965) and Charnov (1980) noted increased levels of young females in *Pandalus borealis* populations after intensive fishery development.

We question what these changes in population structure imply for the future productivity of the pink shrimp resource. The evidence for density-dependent growth argues for a harvest-resistant shrimp stock. Our data also support the hypothesis of Charnov et al. (1978) that the population age structure determines the age of sex change in shrimp. As a consequence of intensive harvest, the age structure has shifted toward younger shrimp. The percentage of primary females has increased, however, resulting in the maintenance of a sexually balanced breeding population. The capacity to accelerate sex change in pink shrimp also increases the stock's ability to withstand harvest pressure, by decreasing the potential for declines in larval production.

Both catch and effort levels in the pink shrimp fishery are continuing to increase. The preliminary total catch for the states of California, Oregon, and Washington is nearly 36,000mt in 1989. The large harvests in 1987–89 (Fig. 11) appear to be the result of a combination of factors. Improved CPUE in 1987 and 1988 (Fig. 2; 1989 data unavailable) indicate some strong year classes of shrimp moving through the fishery. The total harvest levels of age-1 shrimp in these years is

unprecedented in the history of the fishery. The increased size of age-1 shrimp since 1979 has made them more vulnerable to the gear and should have increased the harvest rate on age-1 shrimp relative to 1966–78. Fishing effort in the study area in 1987 and 1988 reached the two highest totals ever recorded, with 1989 likely to be as high or higher. The only other year in which effort approached levels of 1987–88 was in 1980 (Fig. 12). Postulating some improvement in vessel and gear efficiency in the years since 1980, the strong landings of 1987–89 must have been partly a result of record levels of effective fishing effort. In combination, the strong landings, high effort, and dominance of age 1 shrimp in the catch for 1987 and 1988 argue strongly for increased exploitation rates in those years. The large landings in 1989 are probably caused by the same factors.

This raises the question of what impact the increasing harvest of age-1 shrimp may have on the spawning population and subsequent recruitments. A spawner-recruit relationship has not been demonstrated for pink shrimp (Gotshall 1972). However, the Pacific Fishery Management Council (1981) identified some potential indicators of over-harvest of shrimp stocks. These included increases in the percentage of age-1 shrimp in the catch and in the percentage of primary females. In the past, reductions in age-2 and older shrimp were balanced by accelerated sex change in age-1 shrimp, and possibly by increased fecundity at age due to density-dependent growth. Levels of primary females have reached nearly 50% in some years. In such years, pink shrimp are virtually a single-age spawning stock. At some level of exploitation, accelerated sex change and density-dependent growth will not prevent declines in larval release and subsequent recruitment. The strong year-classes passing through the fishery since 1986 indicate that we've probably not reached that level of exploitation as yet.

Acknowledgments

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Between-Reader Bias and Variability in the Age-Determination Process

Daniel K. Kimura
Julaine J. Lyons

Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA
7600 Sand Point Way NE, Seattle, Washington 98115-0070

Abstract.– At the Alaska Fisheries Science Center, one in five age readings produced for routine stock assessments are re-aged independently by a second age-reader. The Center now has a large database of repeated age readings that covers a variety of groundfish species and years. The purpose of this paper is to point out the problems and utility of interpreting such a database. The main problem of interpretation is fundamental, and relates to the fact that the true age of a fish is seldom known. Nevertheless, from a pragmatic point of view, these data can still provide useful insights into the age-determination process. Data from six marine fish species are used to show the overall levels of between-reader bias, agreement, and variability that have occurred on production age readings. Other uses for these data include objectively ranking the relative difficulty in ageing different species, maintaining quality control, examining between-reader differences in ageing criteria, and evaluating the possible importance of between-reader bias and variability in later analysis and modeling applications. Assuming reader bias is negligible, modeling results presented here indicate that estimated percentage agreements are consistent with the hypothesis that age determinations are normally distributed with a constant coefficient of variation over relatively wide age ranges. This result supports use of the coefficient of variation for measuring variability in age precision studies.

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Fishery Bulletin, U.S. 89:53–60 (1991).

In this paper we evaluate a unique database developed for all marine fish species being routinely aged at the Alaska Fisheries Science Center. Here, large subsamples (one in five age readings produced for routine stock assessments) have been re-aged independently by a second experienced age-reader, mainly for the purpose of maintaining quality control. However, it became apparent that this database could be used to provide additional insights into the age-determination process.

Most everyone familiar with the ageing of fish knows this process is fraught with difficulties. At the very least, there must be random variability about some true age. Most likely there is also bias in the ageing methodology at some ages, as well as between-reader differences. Because reader bias is probably affected by the individual reader, the true age of the fish being aged, and perhaps even individual fish, the analysis of repeated age readings made by different readers does not easily fall under the purview of classical statistical theory.

The types of analysis that can be performed on age-determination data are dependent on the kind of data collected and the assumptions the data analyst is willing to make. For example, if replicated readings are made by each reader, it is possible to perform a variance components analysis, assuming that reader effects are random and unbiased (Kimura et al. 1979). Comparative calibration is the area of statistical analysis that compares different methods of measurement (e.g., different readers) where all methods of measurement are assumed to contain error, and perhaps bias (Theobald and Mallinson 1978). Recently Kimura (unpubl.) examined the limits of possible inference for the functional comparative calibration model.

In the analyses presented here we examine between-reader bias and variability based on subsamples aged independently by two age-readers. For these types of data, we define between-reader bias as the average difference $(\bar{a}_1 - \bar{a}_2)$ in ages assigned by these readers when ageing the same specimens of the same nominal age. Thus between-reader bias presumably arises from the two readers using different ageing criteria. If the average difference between age-readers is negligible at some nominal age, then between-reader bias at that age is defined to be negligible, regardless of what the unknown absolute bias of the readers might be.

Estimates of between-reader ageing variability from these types of data can be computed by averaging the sample variances calculated from the two age readings (df = 1) from each age structure over some nominal age. These sample variances (between-reader variances) probably overestimate measurement error, because they include a component of variability that might be thought of as between-reader bias.

Age determination is a statistical process that has a characteristic level of variability. This variability is species-dependent, and provides a basis for comparing the ageing of different

species. For example, a species that can be aged with a larger percentage agreement (percentage of specimens aged the same on two occasions by the same or different reader), or smaller coefficient of variation, provides a statistical confirmation of the statement that species "x" is easier to age than species "y."

Between-reader bias provides a measure of the adequacy of criteria for distinguishing ages in a particular species of some nominal age. Presumably, if there is no between-reader bias, ageing criteria are being applied similarly by both readers, and the data only contain random measurement error. If between-reader bias and measurement error are independent, at this point between-reader variance would also be minimized. Significant between-reader bias may indicate a lack of resolving power in the criteria, insufficient training, or even peculiarities in the structures being aged. Between-reader variance is generally an indicator of overall "ageability," but is not as effective as between-reader bias measurements for pointing out between-reader differences in criteria.

Species often have a characteristic age above which between-reader biases become larger. This age may be interpreted as a line distinguishing which ages are more reliable. For age-readers themselves, between-reader bias is usually of more interest than variability. This is because while measurement error is inherent in the age-determination process, between-reader bias can be controlled to a greater extent.

In age-determination studies the term "precision" is used to describe "agreement," or variability between readings of the same specimen by the same or different age-reader. The term "accuracy" is reserved to describe a comparison of ages generated by readers with the "true" age for specimens of known age.

By emphasizing the importance of between-reader bias and variability, we do not mean to denigrate the obvious importance accuracy and age validation play in the age-determination process (Beamish and McFarlane 1983, 1987). Validation (the comparison of ages determined by counting rings on hard parts with known ages) can be carried out in a variety of ways, all of which are difficult. These include combining an external tag with an oxytetracycline (OTC) injection that labels calcium rings with a mark visible under ultraviolet light, following unusually strong year-classes through time, ageing young fish of known ages, and, most recently, measuring the activity of naturally occurring radioisotopes. Scientists at the Pacific Biological Station (Beamish et al. 1983, Cass and Beamish 1983, Leaman and Nagtegaal 1987, McFarlane and Beamish 1987) have made wide use of the OTC mark. And, recently, two studies appear to have succeeded in validating longevity in rockfish using radioisotopes (Bennett et al. 1982, Campana et al. 1990). Typically, validation can be carried out on only a very few fish. Often, doubts remain concerning criteria for certain age groups, or structures that look different. Nevertheless, the validation process is a critical one, and age-readers must constantly strive to improve the accuracy of their age determinations.

Because we seldom knew the true age of a fish, absolute bias and total mean-square error in the ageing process were not known. Therefore, our discussions here will be limited to between-reader bias and variability. These quantities are defined by the between-reader bias and coefficient-of-variation formulas described in the following section.

Materials and methods

The Ageing Unit at the Alaska Fisheries Science Center has the broad responsibility of ageing commercially important fish species and fish stocks in U.S. waters from California to the eastern Bering Sea. Historically, data have been accumulated from three principal sources: scientific surveys using various fishing gear, and foreign and domestic vessels fishing in U.S. waters. The present data consist of ages read from the otoliths (ear bones) of various groundfish species collected using assorted gear.

Since 1981, the preferred method of reading ages from these structures has been to either break or saw the otolith cross-wise, burn the exposed surface, and read the cross-section under a microscope (Chilton and Beamish 1982). Only young or unusually clear specimens of select species can be read from the intact surface.

In 1983 a quality-control program was initiated wherein 20% of all routine age readings would be independently re-aged by an age-reader (i.e., the tester) particularly experienced in a species. Statistics were calculated on these reader/tester data (one reading per otolith from each age-reader) in the following manner:

1 mean ($\bar{x}$) = (tester + reader)/2.
2 standard deviation (SD) = $\sqrt{[(\text{tester} - \bar{x})^2 + (\text{reader} - \bar{x})^2]}$
3 nominal age (age): $\bar{x}$ (rounded), or tester age
4 n (count): sample size (number of specimens aged)
5 percentage agreement: (n agree/n) × 100
6 coefficient of variation (CV) = (SD/$\bar{x}$) × 100
7 between-reader bias: reader age − tester age
8 percentage bias: [(reader age − tester age)/$\bar{x}$] × 100

Elements 5–8 were averaged over the "n" specimens of the same nominal age, and over all ages (weighted by n) for overall statistics.

Table 1
Statistics comparing reader/tester data for Pacific whiting in 1986. Bias is between-reader bias; nominal age is mean.

Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias
2	258	100.0	0.0	0.00	0.0
3	58	50.0	15.1	−0.14	−5.3
4	8	62.5	7.6	−0.38	−10.7
5	13	92.3	3.6	0.23	5.1
6	651	95.5	0.6	−0.00	−0.2
7	118	20.3	9.9	0.23	3.4
8	66	37.9	11.9	−0.23	−2.9
9	153	77.8	2.4	−0.02	−0.2
10	28	10.7	12.1	0.25	2.4
11	23	26.1	12.0	0.00	−0.2
12	13	0.0	12.0	−0.92	−7.9
13	29	75.9	1.4	0.03	0.3
14	11	0.0	6.1	0.45	3.3
15	4	25.0	13.1	0.25	1.5
16	2	100.0	0.0	0.00	0.0
Average		78.6	3.2		

When the main purpose of an analysis is to compare criteria of the age readers, the nominal age for classification should be the tester age. When the overall characteristics of ageing a species is of interest, perhaps $\bar{x}$ is the better nominal age. The estimated statistics by age look different depending on which nominal age is being used. For example, if $\bar{x}$ is used, the percentage agreement for younger ages will appear larger.

Both the average percent error (Beamish and Fournier 1981) and the coefficient of variation have been proposed as an "age independent" method of estimating precision for age-determination studies. Assuming normality, Chang (1982) favored the coefficient of variation on the basis of efficiency, and we favor the coefficient of variation on the basis of common usage. Under differing distributional assumptions, the average percent error may actually be superior.

If age determinations are independently and normally distributed about some true age, then the percentage agreement at each age can be predicted from the area under the normal curve. Suppose the age of an "a"-year-old fish can be determined with a certain coefficient of variation. The difference between two independent age determinations (b and c, say), would be distributed as

$$z = b - c \sim N[0, 2CV^2a^2].$$

The predicted percentage agreement (ppa) at age "a" is then

$$ppa = [\Phi(z_2) - \Phi(z_1)] \times 100,$$

Table 2
Statistics comparing reader/tester data for yellowfin sole in 1986. Bias is between-reader bias; nominal age is mean.

Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias
3	1	100.0	0.0	0.00	0.0
4	4	50.0	10.1	0.50	14.3
5	11	45.5	9.7	0.64	13.7
6	15	86.7	1.7	0.13	2.4
7	64	79.7	2.2	0.14	2.2
8	32	68.8	2.9	0.06	0.8
9	23	78.3	1.8	−0.13	−1.5
10	39	66.7	2.7	0.21	2.1
11	19	57.9	3.2	−0.16	−1.5
12	32	62.5	3.0	0.25	2.1
13	19	52.6	3.3	−0.05	−0.4
14	14	42.9	6.9	0.79	5.7
15	22	68.2	2.2	0.45	3.1
16	26	34.6	3.6	0.04	0.2
17	12	25.0	5.3	0.08	0.5
18	16	43.8	3.0	0.38	2.2
19	12	58.3	1.9	0.33	1.8
20	5	0.0	7.1	0.00	0.0
23	3	0.0	5.1	−1.00	−4.3
25	1	0.0	2.9	1.00	4.1
26	1	0.0	2.8	1.00	3.9
Average		60.9	3.2		

where Φ = the cumulative distribution function of the unit normal distribution,
$z_1 = -0.5/[(1.4142)(CV)(a)]$ and,
$z_2 = +0.5/[(1.4142)(CV)(a)]$.

Results and discussion

The above statistics were calculated for several species sampled in 1986 and subsequently aged (Tables 1–6). These are overall statistics calculated using data from all readers and testers, and therefore represent group rather than individual performance. A summary of percentage agreements and coefficients of variation averaged over all ages is given below:

Species	Percentage agreement	CV
Pacific whiting *Merluccius productus*	78.6	0.032
yellowfin sole *Limanda aspera*	60.9	0.032
Pacific ocean perch *Sebastes alutus*	40.8	0.049
walleye pollock *Theragra chalcogramma*	63.8	0.050
Atka mackerel *Pleurogrammus monopterygius*	66.8	0.068
sablefish *Anoplopoma fimbria*	43.7	0.129

Table 3

Statistics comparing reader/tester data for Pacific ocean perch in 1986. Bias is between-reader bias; nominal age is mean.

Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias	Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias
2	1	100.0	0.0	0.00	0.0	34	2	0.0	12.7	1.00	3.0
3	7	71.4	8.1	0.29	11.4	36	1	0.0	3.9	−2.00	−5.6
4	1	0.0	20.2	1.00	28.6	37	2	0.0	1.9	1.00	2.7
5	34	73.5	4.2	−0.03	−0.7	38	3	66.7	0.6	0.33	0.9
6	29	51.7	6.2	−0.28	−5.0	39	5	0.0	8.0	0.80	2.0
7	9	33.3	10.7	−0.78	−11.7	40	2	0.0	2.7	−1.50	−3.8
8	62	71.0	2.9	0.02	0.2	41	8	12.5	2.2	−0.50	−1.2
9	42	45.2	4.7	0.05	0.5	42	6	50.0	1.7	0.00	0.0
10	41	36.6	5.8	0.20	2.1	43	4	25.0	3.7	0.75	1.7
11	12	25.0	7.7	0.33	3.1	44	1	0.0	4.9	3.00	6.9
12	21	38.1	5.2	0.19	1.6	45	3	66.7	1.0	0.67	1.5
13	6	16.7	7.3	−0.67	−5.2	46	3	0.0	2.1	−0.67	−1.4
14	8	0.0	6.5	−1.00	−7.3	47	1	0.0	3.0	2.00	4.3
15	9	33.3	5.3	0.44	3.0	48	1	100.0	0.0	0.00	0.0
16	14	21.4	4.8	0.50	3.2	49	1	0.0	1.5	1.00	2.1
17	5	20.0	5.0	0.40	2.4	50	2	0.0	1.4	0.00	0.0
18	7	14.3	6.8	0.00	−0.0	52	5	0.0	7.4	4.20	8.1
19	8	37.5	7.0	1.13	5.9	54	2	0.0	2.6	−1.00	−1.9
20	7	28.6	4.6	−0.71	−3.7	55	2	50.0	3.2	−2.50	−4.6
21	1	0.0	10.3	3.00	14.6	56	1	0.0	3.8	3.00	5.4
22	1	100.0	0.0	0.00	0.0	57	2	0.0	7.4	−6.00	−10.5
23	2	0.0	6.1	0.00	0.0	59	3	0.0	6.0	−3.00	−5.1
24	2	50.0	1.5	−0.50	−2.1	60	1	0.0	2.4	−2.00	−3.3
25	4	25.0	4.3	−1.50	−6.1	61	5	0.0	2.8	−1.60	−2.6
26	2	0.0	2.8	0.00	0.0	65	2	50.0	1.6	−1.50	−2.3
27	3	33.3	3.6	1.33	5.0	66	1	0.0	1.1	−1.00	−1.5
28	2	100.0	0.0	0.00	0.0	68	1	0.0	3.1	3.00	4.4
29	2	0.0	17.1	3.00	10.3	72	1	0.0	1.0	1.00	1.4
30	1	0.0	4.7	2.00	6.7	73	1	0.0	8.8	9.00	12.4
31	2	0.0	4.6	0.00	0.0	75	1	100.0	0.0	0.00	0.0
32	2	0.0	4.4	0.00	0.0	78	1	0.0	3.6	−4.00	−5.1
33	1	100.0	0.0	0.00	0.0	Average		40.8	4.9		

Table 4

Statistics comparing reader/tester data for pollock in 1986. Bias is between-reader bias; nominal age is mean.

Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias
1	18	100.0	0.0	0.00	0.0
2	64	93.8	2.9	0.03	2.1
3	132	92.4	2.1	0.00	0.0
4	159	74.8	5.3	0.04	1.0
5	136	66.2	5.6	0.07	1.5
6	119	64.7	5.2	0.06	1.1
7	113	49.6	6.5	−0.19	−2.7
8	181	56.9	4.7	−0.19	−2.5
9	85	21.2	7.1	0.11	1.2
10	26	15.4	10.7	−0.08	−0.8
11	17	41.2	7.4	0.41	3.8
12	8	25.0	5.3	−0.38	−3.2
13	2	0.0	8.3	−0.50	−3.7
Average		63.8	5.0		

Table 5

Statistics comparing reader/tester data for Atka mackerel in 1986. Bias is between-reader bias; nominal age is mean.

Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias
1	15	100.0	0.0	0.00	0.0
2	76	97.4	1.2	0.00	0.0
3	47	55.3	14.2	0.02	0.9
4	28	64.3	10.3	−0.11	−2.8
5	29	48.3	10.1	0.03	1.1
6	28	50.0	6.8	0.11	1.8
7	20	65.0	5.4	−0.40	−6.0
8	35	40.0	7.2	−0.26	−3.4
9	4	25.0	8.1	0.00	0.3
10	4	50.0	3.7	−0.50	−5.3
Average		66.8	6.8		

Table 6

Statistics comparing reader/tester data for sablefish in 1986. Bias is between-reader bias; nominal age is mean.

Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias
1	13	100.0	0.0	0.00	0.0
2	43	88.4	5.5	0.02	1.6
3	43	58.1	13.4	−0.21	−7.8
4	24	58.3	10.1	−0.25	−7.1
5	49	53.1	10.2	0.51	10.8
6	50	34.0	12.7	0.82	14.4
7	29	37.9	12.1	0.79	11.7
8	17	11.8	15.0	1.18	15.2
9	21	0.0	20.6	2.33	26.9
10	11	0.0	24.2	3.00	30.3
11	11	9.1	17.4	1.73	16.0
12	12	8.3	24.1	3.83	32.7
13	5	0.0	29.9	5.40	42.3
14	4	0.0	36.7	4.50	33.3
15	1	0.0	4.9	1.00	6.9
16	1	0.0	31.9	7.00	45.2
18	2	0.0	8.1	1.00	5.7
19	2	0.0	35.5	9.50	50.2
23	1	0.0	15.7	−5.00	−22.2
29	2	50.0	1.2	0.50	1.8
Average		43.7	12.9		

Table 7

Statistics comparing reader/tester data by individual readers for pollock in 1986. Reader A is less experienced than reader B. Bias is between-reader bias; nominal age is tester age.

Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias
Results for Reader A					
1	21	85.7	6.7	0.14	9.5
2	46	87.0	4.1	0.09	2.9
3	95	80.0	4.2	0.16	4.3
4	94	72.3	4.9	0.02	−0.3
5	76	69.7	4.2	0.09	1.2
6	59	62.7	4.8	0.07	0.5
7	63	38.1	7.5	−0.17	−3.5
8	122	44.3	6.0	−0.18	−3.0
9	30	26.7	10.0	−0.30	−5.0
10	5	0.0	7.4	−1.00	−10.5
11	3	0.0	6.7	−1.00	−9.5
12	5	20.0	12.5	−1.80	−17.6
13	1	0.0	11.8	−2.00	−16.7
14	1	0.0	10.9	−2.00	−15.4
Average		61.0	5.5		
Results for Reader B					
2	11	100.0	0.0	0.00	0.0
3	30	86.7	3.2	0.00	−0.8
4	57	80.7	3.3	0.05	0.7
5	34	76.5	4.0	0.06	0.4
6	44	79.5	2.8	0.00	−0.4
7	35	80.0	2.0	0.09	1.0
8	54	74.1	2.5	−0.02	−0.5
9	29	24.1	7.1	−0.28	−3.8
10	8	50.0	5.3	0.00	−0.6
11	14	50.0	6.0	−0.57	−6.0
12	3	33.3	3.9	0.00	−0.2
Average		72.4	3.4		

Because percentage agreement decreases with the age of fish (Tables 1–6), and age distributions vary greatly among different species and among samples of the same species, percentage agreement lends itself only to age-specific comparisons. This is illustrated above by Pacific ocean perch and sablefish which show a similar percentage agreement; however, Pacific ocean perch is much more "ageable" than sablefish, as reflected in the corresponding coefficients of variation.

Although percentage agreement and coefficient of variation both reflect the relative difficulty of ageing each species, only the coefficient of variation adjusts for the absolute age of the fish. Therefore, one might conclude that the easiest species to age are Pacific whiting (Table 1) and yellowfin sole (Table 2); and the medium-difficult species are Pacific ocean perch (Table 3) and walleye pollock (Table 4).

The most difficult species to age—species with unresolved criteria, or species for which readers needed further training—were Atka mackerel (Table 5) and sablefish (Table 6). In fact, in this study the age-reader for Atka mackerel was inexperienced with the species, and there were unresolved criteria for sablefish.

The most important usage of reader/tester data is in maintaining quality control. Unlike the data presented in Tables 1–6, for quality-control purposes we need to compare only one tester with one reader, with the nominal age being the tester age. For pollock (Table 7) there were significant between-reader biases at older ages in the case of inexperienced reader A. There were no such between-reader biases for the experienced reader B. To ensure data quality, these types of between-reader biases are constantly reviewed and the samples partially re-aged, before the data are released for use.

Sablefish is an especially difficult species to age (Table 8). There were so many problems with age determination that we suspended ageing, reviewed criteria with other ageing labs, and re-aged several large samples. It is probable that between-reader bias for this species can be reduced, but it is doubtful that the coefficient of variation for this species can be substantially reduced. Nevertheless, the availability of reader/tester data was useful in revealing problems. Also, data users deserve a quantitative presentation of variability in age determinations and may be able to use these

Table 8

Statistics comparing reader/tester data for individual Reader A ageing sablefish in 1986. Bias is between-reader bias; nominal age is tester age.

Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias
1	16	81.3	8.8	0.19	12.5
2	47	80.9	7.3	0.19	4.6
3	40	62.5	10.9	−0.08	−6.6
4	41	34.1	14.7	0.68	12.5
5	62	41.9	14.1	0.82	10.0
6	40	42.5	12.2	1.05	12.7
7	29	37.9	11.9	1.28	14.6
8	23	8.7	21.6	2.83	24.2
9	15	0.0	21.4	2.87	23.7
10	6	0.0	14.4	1.67	13.3
11	8	12.5	15.6	2.88	17.2
12	6	16.7	13.3	1.17	6.4
14	1	0.0	4.9	1.00	6.9
16	2	0.0	19.2	−1.00	−9.9
17	1	0.0	11.5	3.00	16.2
18	1	0.0	4.0	−1.00	−5.7
25	1	0.0	15.7	−5.00	−22.2
28	1	0.0	2.5	1.00	3.5
29	1	100.0	0.0	0.00	0.0
Average		43.7	12.9		

data for making decisions on aspects of their data analysis and modeling.

We examined the question of consistency between the percentage agreement and coefficient of variation measures of variability when analyzing between-reader data. Earlier we showed that assuming a constant coefficient of variation, and the normal error model, the percentage agreement can be predicted for all nominal ages. By comparing these theoretical curves with estimated percentage agreements calculated from data (Tables 1–6), some confidence in the consistency of the two measures can be derived. However, this comparison is crude due to the probable existence of between-reader biases that are not factored into the analysis.

Four different values for the coefficients of variation were used to calculate theoretical percentage agreement curves (Fig. 1A). These curves were then compared with estimated percentage agreement values for yellowfin sole (CV = 0.032, Fig. 1B), walleye pollock (CV = 0.050, Fig. 1C), and sablefish (CV = 0.129, Fig. 1D).

The percentage agreements for all three species appear consistent with the hypothesis that the coefficient of variation is constant over a wide age range, although the percentage agreements for pollock are biased low. These results support averaging the coefficient of variation across age ranges, and generally support using the coefficient of variation for interpreting precision data from age-determination studies. However, there is considerable variation in these data which makes our results somewhat tentative.

An important factor that also affects the ageing process is the presence of a strong year-class. For example, if two adjacent year-classes have absolute strengths of 10 and 100 fish, a 10% imprecision of ±1 year will add 5 fish from the strong cohort to the weak one (a 50% change) but only one-half a fish from the weak year-class to the strong (a 0.5% change). The data on Pacific whiting (Table 1) show how this phenomenon can lead to poor percentage agreements for weaker year-classes.

Users of age data are often concerned that after some age, say 9 years, for example, the dominant year-classes become spread over several ages. Since percentage agreement by such an age has often decreased to 50% or less, it is expected that age distributions will be smoothed. The only reason the ages would not be smoothed is if the dominant year-class is being anticipated by the age-reader. For example, if samples are 90% 10-year-olds, it would be difficult for the age-reader not to anticipate that age and between-reader agreement would be high. However, if say 9-, 10-, and 11-year- olds occur in equal numbers, the agreement would not be nearly as good.

Two possible ways of handling this problem are evident. A controversial method would be to assure that all age-readers are reasonably coached as to the probable occurrence of a strong year-class; the other is to group the older ages in any model analyzing these data (e.g., Deriso et al. 1989). Both approaches avoid asking the age-reader to perform the impossible.

Finally, interpretation and analysis of repeated readings given here assume that the repeated readings were statistically independent. In the present context, this simply means that each reader did not have information regarding the other reader's results. When repeated readings are not made on an independent basis, or are of inadequate sample size, the data will be difficult or impossible to interpret statistically. From such a database, it is impossible to make assertions regarding precision.

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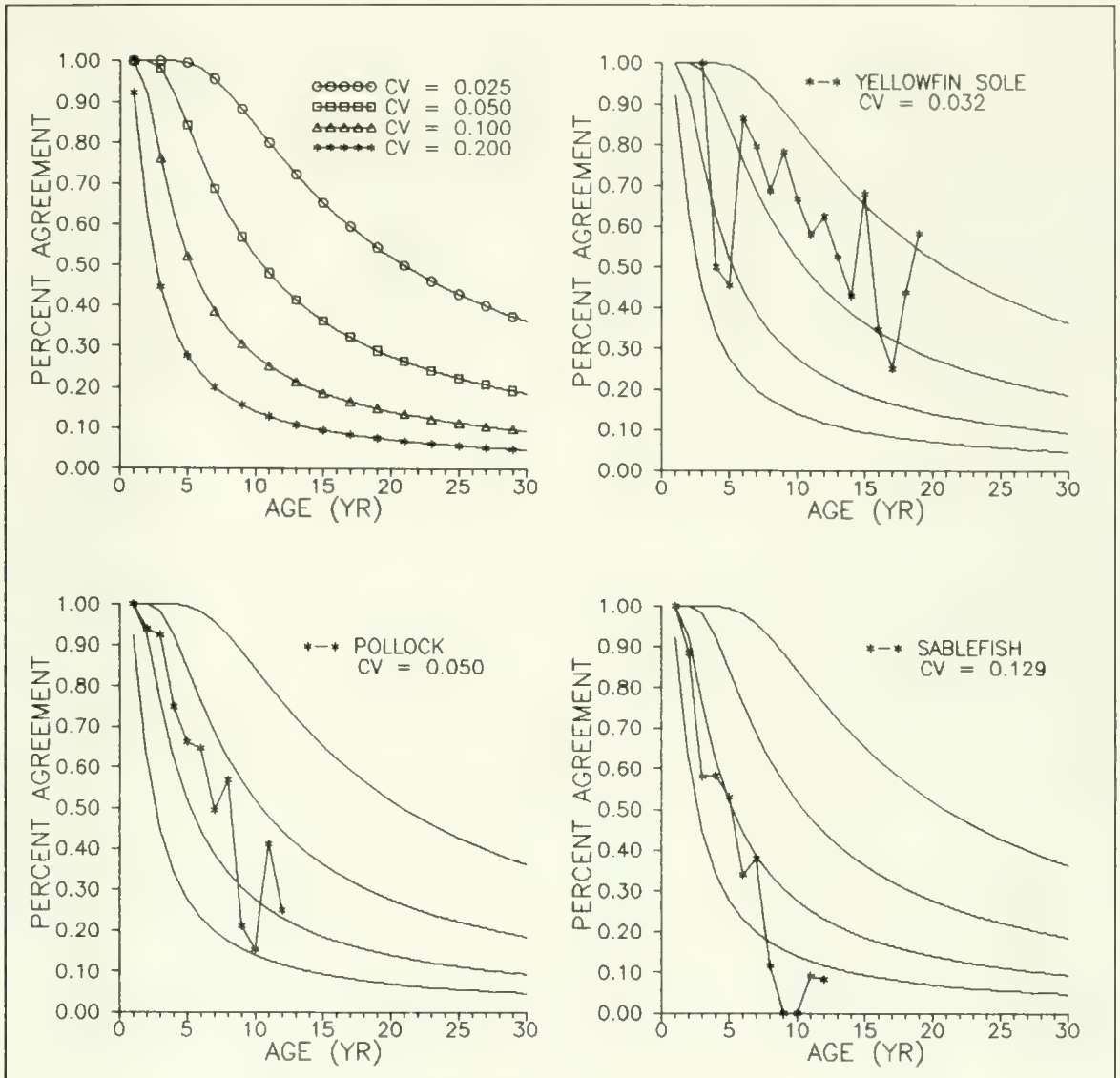

Figure 1

Predicted percentage agreement curves assuming different coefficients of variation and normally distributed error (upper left); overlayed with estimated percentage agreements for yellowfin sole (upper right); overlayed with estimated percentage agreements for pollock (lower left); and overlayed with estimated percentage agreements for sablefish (lower right).

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Survival and Growth of Early-Juvenile American Lobsters *Homarus americanus* Through Their First Season While Fed Diets of Mesoplankton, Microplankton, and Frozen Brine Shrimp

Kari L. Lavalli

Boston University Marine Program, Marine Biological Laboratory
Woods Hole, Massachusetts 02543

Abstract.—Early juvenile (Stages V–IX) American lobsters *Homarus americanus* were fed diets of mesoplankton in filtered seawater, meso/microplankton combination in filtered seawater, and frozen brine shrimp in both filtered and unfiltered seawater to determine if mesoplankton diets could sustain survival and growth throughout most of the first year of molts and if smaller zooplankters and phytoplankton in the meso/microplankton diet could be utilized as food and could sustain survival in periods of low food supply. At the beginning of the experiment, there were no significant differences in either carapace length or weight between the groups of sibling lobsters. Lobsters fed mesoplankton had high survival (80%) and significant increases in both carapace length and weight, although they weighed less at Stage IX than those fed frozen brine shrimp in unfiltered seawater. Lobsters fed frozen brine shrimp in filtered seawater had low survival (15%), but did not differ significantly at Stage IX from those fed mesoplankton in terms of both carapace length and weight. Lobsters fed brine shrimp in unfiltered seawater had high survival rates (95%) and weighed nearly twice as much at Stage IX than both the brine shrimp-fed lobsters in filtered seawater and the mesoplankton-fed lobsters; however, none of these three surviving groups differed significantly in carapace length at Stage IX. Intermolt periods for the three surviving groups were not significantly different until the molt between Stage VIII and IX when the mesoplankton-fed lobsters took nearly twice as long to molt as either of the brine shrimp-fed groups. Lobsters fed meso/microplankton did not molt out of Stage V and died within 36 days of the 107-day experiment. These results indicate that mesoplankton diets promote growth and survival of lobsters throughout most of their first season of molting and that larger planktonic organisms may contain essential nutritional requirements not met by brine shrimp alone. However, the meso/microplankton diet, consisting mostly of diatoms, does not provide sufficient nutrition for survival during periods of starvation.

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Little is known of the natural foraging activities of the settled postlarvae (Stage IV) and early-juvenile (<1 year-old) stages of the American lobster *Homarus americanus*, presumably due to the inability of past investigators to locate them in the benthic environment. Recently, Barshaw and Bryant-Rich (1988) examined the behavior of the early-juvenile American lobster in naturalistic settings in the laboratory and found that they spent a considerable amount of time pleopod fanning (15% of the time) and antennule flicking (15–40% of the time) at the entrance of their burrows. During their 8-month investigation, Barshaw and Bryant-Rich never observed an early-juvenile lobster leave its burrow; of the several instances where lobsters were seen feeding, they captured amphipods near the entrance of the burrow twice while other observations indicated that the lobsters were capturing planktonic organisms via self-generated currents which drew the organisms toward the burrow entrance. Their observations are corroborated by field cage studies of Gregory Roach (Nova Scotia Dep. Fish., Halifax, N.S., Canada B3J 3C4, pers. commun., Nov. 1989) where he, too, never observed early-juvenile American lobsters leave their burrows during one year of observations.

While little is known about the natural diet of recently settled American lobsters, Cobb et al. (1983) observed presettlement Stage-IV American lobsters capturing crab megalopae and insects in the field. Stomach content analyses indicate that the Stage-IV diet is similar to that of the larvae, consisting of copepods, decapod larvae, amphipods, algae, and diatoms (Williams 1907, Herrick 1911, Templeman and Tibbo 1945). Although most laboratory investigations have used artificial feeds which wild early-juvenile lobsters would never encounter, some studies have provided information on naturalistic diets. Emmel (1908) found that Stage-IV American lobsters were capable of surviving on planktonic organisms obtained from the water alone. The intermolt period for this group of lobsters was significantly longer than that for groups fed on beef, soft-shelled clam, lobster muscle, or shredded fish, but this result was probably due to differences in the overall amount of food available to the groups, as unequal weights of food were used. More recently, Andrea (1975), D'Agostino (1980), and Good et al. (1982) found that when amphipods were used as a food source, growth rates of larval, postlarval, and early-juvenile American lobsters improved significantly over brine shrimp diets (both live and

frozen) and artificially prepared compound diets. Daniel et al. (1985) demonstrated that Stage-IV and early-juvenile American lobsters were capable of surviving and growing on a frozen filtrate diet consisting of 99% barnacle larvae and 1% calanoid copepods; however, these filtrate-fed lobsters were significantly smaller (by 17%) than lobsters fed on frozen adult brine shrimp. Similarly, Barshaw (1989) found that Stage-IV American lobsters were also capable of surviving and growing through two molts on a diet of live, unidentified plankton (size 152–1000 μm), although the plankton-fed lobsters were smaller and had a greater intermolt period from Stage V to VI than those fed on frozen brine shrimp. In all of the above studies, there were no differences in mortality between the different groups of fed lobsters.

This study examined the survival and growth of early-juvenile (Stages V–IX) American lobsters fed on diets of mesoplankton (95–1000 μm) and a meso/microplankton combination (25–95 μm) while using frozen brine shrimp diets for reference. Studies with other crustaceans indicate that phytoplankton may be used as a supplement when zooplankton abundance is low and its presence may extend the period of survival over that observed for starved animals (McConaugha 1985). However, the nutritional value of phytoplankton is highly dependent on its content of essential fatty acids which can vary in response to temperature, dissolved nutrients, light, and age (Castell and Kean 1986). While American lobsters have not been classified as algal feeders (Lebour 1922), stomach content analyses of the larvae and postlarvae indicate that diatoms and other algae form part of their diet (Herrick 1895, Williams 1907, Herrick 1911). Recently, Lavalli and Barshaw (1989) have shown that Stage-IV and -V American lobsters are capable of removing particles from the water column to at least a size of 70 μm, indicating that early-juvenile lobsters may be able to utilize small organisms in the mesoplankton and microplankton. This study was designed, in particular, to determine two things: (1) Whether early juveniles could utilize an already-proven diet (mesoplankton) for Stage-IV and -V lobsters throughout much of their first season of molting activity, and (2) whether early juveniles could extend survival by utilizing the organisms found in the smaller range of mesoplankton and in the microplankton.

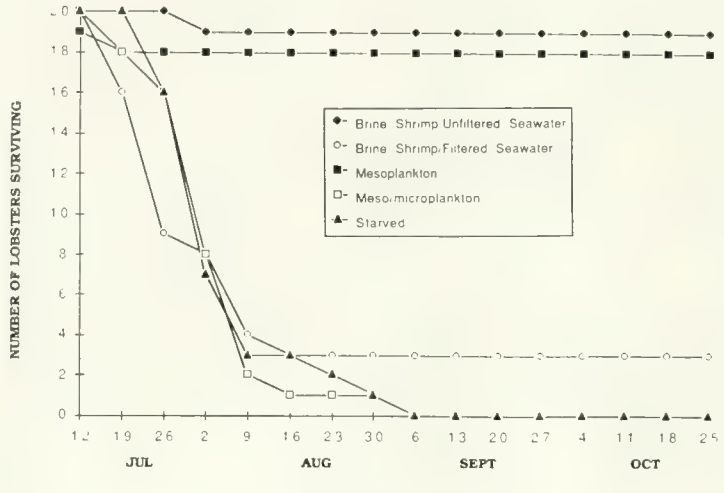

Figure 1

Mean number of original 20 lobsters surviving through the 107 days of the experiment (molt stages V–IX) on each of the diet regimes: brine shrimp in unfiltered seawater, brine shrimp in filtered seawater, mesoplankton (95–1000 μm) in filtered seawater, meso/microplankton combination (25–95 μm) in filtered seawater, and starved.

Materials and methods

Prior to the beginning of the experiment, Stage-IV American lobster siblings *Homarus americanus* were held collectively in a seawater table supplied with ambient, unfiltered seawater and were fed *ad libitum* on frozen adult *Artemia* (San Francisco Bay type). Siblings were used for the experiment, since genetic differences between females can produce significant differences in weight among similarly raised juvenile lobsters (Conklin et al. 1975, Hedgecock and Nelson 1978). The lobsters were then randomly assigned to one of four groups of 20 animals: a mesoplankton-fed group (95–1000 μm), a meso/microplankton combination-fed group (25–95 μm), a frozen brine shrimp-fed group, and a starved group. Upon assignment, individual lobsters were placed into plastic trays (Rubbermaid Drawer Organizers, No. 2915) with dimensions 224 mm long × 75 mm wide × 50 mm deep, and volume of ~750 mL. Each tray was modified to include a sidewall screen for water flow and a dark-grey PVC tube (10 mm diameter) glued to the bottom which could act as a shelter. The trays were provided with ambient seawater which was filtered with a dual-cartridge filtering system (a 50-μm honeycomb filter followed by a 5-μm nominal filter). They were arranged in a Latin square design to intersperse the treatments and were kept in darkness, except during cleaning and feeding periods, as previous investigations demonstrated that juvenile lobsters

grew more quickly and were more active in a nearly constant dark regime (Bordner and Conklin 1981). The water flow to the trays was turned off for 1 hour after the introduction of food to allow the lobsters to more easily capture the food. Filters were replaced during these feeding periods if they were clogged.

Lobsters were fed according to group; excess food and other debris were removed daily with a kitchen baster. All trays were thoroughly scrubbed each week to remove algal growth from the sidewalls and bottom. During cleaning the lobsters were held in a moist, small-mesh fish net. Every attempt was made to feed equal wet weights of food, and representative portions of each diet were weighed each week. For the plankton diets, representative portions were also photographed using the technique of silhouette photography (Edgerton 1977, Ortner et al. 1979) so that identification of the planktonic organisms could be made without the aid of a microscope.

Plankton was collected three to four times per week by towing with a #10 plankton net (152 μm) and a phytoplankton net (25 μm) in the Waquoit Bay/Nantucket Sound areas. After collection it was sieved to remove objects >1000 μm and to divide the plankton into each size group. Half of the plankton was used immediately while the other half was refrigerated overnight and used the following day.

Carapace lengths of Stage-V lobsters were measured to the nearest 0.1 mm using calipers, and their weights were recorded on a Brainweigh B300D scale to the nearest 0.001 g. The lobsters were blotted with absorbent paper to remove excess water prior to weighing. The experiment ran until all surviving lobsters attained Stage IX. During this time, the dates for all molts (for the determination of intermolt periods) and deaths were recorded. Although no post-mortems were performed, it was noted whether lobsters died in the process of molting or of unknown causes. Coloration of the lobsters was also noted. After achieving Stage IX, the lobsters were once again measured and weighed.

During the time of this experiment, a fifth group of lobsters (also siblings of the other four groups of lobsters) was raised in seawater tables for another experiment. The lobsters in this fifth group were placed individually into separate circular containers (85 mm diameter; 200 mm high) consisting of a black plastic bottom glued to a cylinder made of screening (1-mm mesh). These lobsters were fed the same amount of brine shrimp as the brine shrimp group of lobsters above, but lived in unfiltered, ambient seawater and were subject to ambient daylight plus overhead fluorescent lighting. Organic debris was cleaned out of the seawater table and containers at least once per month. While data on the initial (Stage V) weights and carapace lengths are unavailable for this fifth group of lobsters, their final (Stage IX) weight and carapace length were recorded. Intermolt periods were recorded except for the period between Stages V and VI, since this group was held communally until after they had molted into Stage V.

Data for each of the measurements taken (intermolt period, initial (Stage V) and final (Stage IX) carapace lengths and weights) were analyzed using the Student's t-test when comparisons between two groups or two measurements within a group (i.e., initial and final weights or carapace lengths) were made, and by 1-way ANOVA tests when more than two groups were compared. Where ANOVA tests indicated significant differences were present, the groups were compared to determine which groups were different by using the Tukey test with unequal sample sizes. Differences in survival rates were tested with a 2×2 chi-square contingency table. This experiment was conducted at the Marine Biological Laboratory in Woods Hole, MA from 13 July to 27 October 1987. The ambient seawater temperature ranged from 23 to 14.5°C and averaged 19.6°C.

Results

Survival was high in the groups fed brine shrimp in unfiltered seawater (95% survival), brine shrimp in filtered seawater (95% survival), and mesoplankton (90% survival) for the molt between Stage V and VI. During the subsequent molts, however, the group fed brine shrimp in filtered seawater had significantly higher mortality (χ^2, $P<0.001$; Fig. 1), with only 15% survival by the end of the experiment. The survival of the brine shrimp-fed group in unfiltered seawater remained unchanged, while that of the mesoplankton-fed group fell to 80% by the end of the experiment. However, there was no significant difference in survival between these two groups. Of the deaths noted for each of the groups, one lobster fed brine shrimp in unfiltered seawater and one fed mesoplankton died during its molt; of the 17 lobsters which died on the brine shrimp diet in filtered seawater, 14 died while in the process of molting. Coloration of the surviving groups differed, with the brine shrimp-fed group in filtered seawater being pale blue, typical of brine shrimp-fed lobsters, and the mesoplankton-fed group and brine shrimp-fed group in unfiltered seawater being the wild-type coloration.

None of the starved or meso/microplankton combination-fed lobsters molted beyond Stage V. All of the lobsters in these two groups died within 36 days of the 107-day experiment, and although the lobsters fed the meso/microplankton combination diet took slightly

longer to die (23.842 ± 10.035 (SD) days vs. 21.75 ± 7.063 days), this difference was not significant.

Intermolt duration data (Fig. 2) showed that the brine shrimp-fed group in filtered seawater took significantly longer to molt (by 1 day) into Stage VI than the mesoplankton-fed group (10.412 ± 1.502 days vs. 11.389 ± 1.243 days; Student's t-test, $P<0.025$). Data are not available on the intermolt period between Stages V and VI for the brine shrimp-fed group in unfiltered seawater. There was no significant difference between the groups brine shrimp-fed in filtered seawater, brine shrimp-fed in unfiltered seawater, and mesoplankton-fed for the intermolt periods between Stages VI and VII (14.857 ± 2.035 vs. 13.444 ± 1.653 vs. 14.059 ± 1.853 days) and Stages VII and VIII (22.0 ± 7.810 vs. 20.556 ± 4.681 vs. 20.529 ± 2.528 days). However, the intermolt periods of both brine shrimp-fed groups were significantly different (18.0 ± 1 and 16.842 ± 2.292 days; 1-way ANOVA, $P<0.001$; Tukey test, $P<0.001$) from those of the mesoplankton-fed group (36 ± 5.057 days) for the molt between Stages VIII and IX, with the two brine shrimp-fed groups taking nearly half the time of the mesoplankton-fed group to molt into Stage IX.

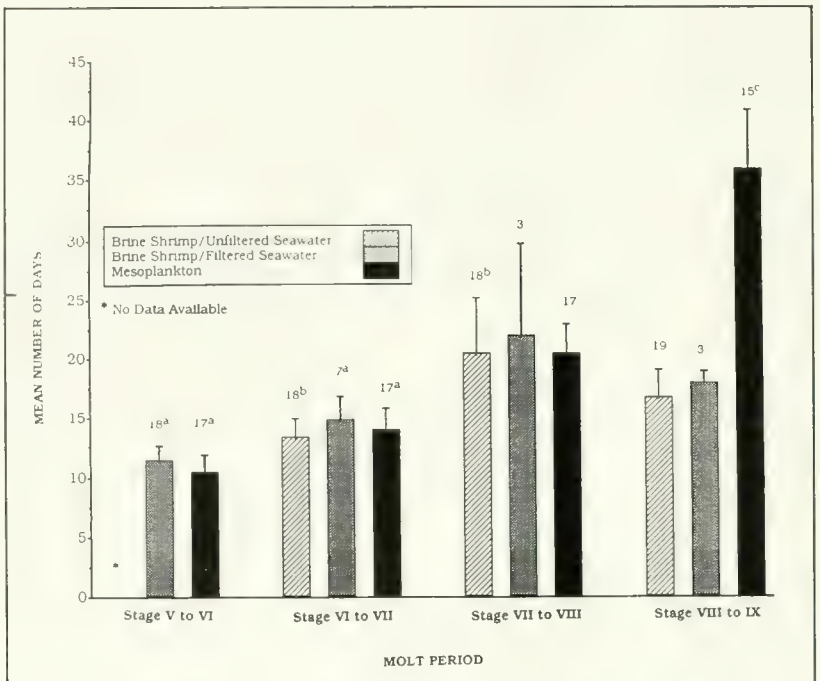

Figure 2

Mean intermolt durations for lobsters on each of three diet regimes: brine shrimp in unfiltered seawater, brine shrimp in filtered seawater, and mesoplankton (95–1000 μm) in filtered seawater. Bars indicate standard deviation values. ([a]) Stage VI molt date missed for one lobster, so intermolt period could not be determined for Stages V–VI and VI–VII for that lobster. ([b]) Stage VII molt date missed for one lobster, so intermolt period could not be determined for Stages VI–VII and VII–VIII for that lobster. ([c]) Stage IX molt date missed for one lobster, so intermolt period could not be determined for Stages VIII–IX for that lobster.

There was no significant difference between any of the groups brine shrimp-fed in filtered seawater, mesoplankton-fed, meso/microplankton combination-fed, and starved lobsters at the beginning of the experiment in either weight (0.06 ± 0.011 vs. 0.066 ± 0.011 vs. 0.059 ± 0.009 vs. 0.061 ± 0.011 g, respectively; Fig. 3) or carapace length (4.66 ± 0.214 vs. 4.761 ± 0.214 vs. 4.739 ± 0.236 vs. 4.716 ± 0.236 mm respectively; Fig. 4). Although measurements are not available for the brine shrimp-fed group in unfiltered seawater, they probably did not differ significantly from the other groups since they were maintained in conditions identical to their siblings until immediately before the molt to Stage V. Each of the surviving groups of lobsters fed brine shrimp in filtered seawater, brine shrimp in unfiltered seawater, and mesoplankton showed significant growth (Student's t-test, $P<0.001$) in terms of both increased weight and carapace length (Figs. 3 and 4). However, final (Stage IX) weights did differ between groups (1-way ANOVA, $P<0.001$). The weight of the brine shrimp-fed group in unfiltered seawater (0.837 ± 0.117 g) was significantly greater (Tukey test, $P<0.001$) than that of both the brine shrimp-fed group in filtered seawater (0.484 ± 0.183 g) and the mesoplankton-fed group (0.484 ± 0.037 g). However, there was no significant difference between the latter two groups. Final (Stage IX) carapace lengths did not differ between the three surviving groups (brine shrimp-fed in filtered seawater, 9.9 ± 1.353 mm; brine shrimp-fed in unfiltered seawater, 10.459 ± 0.564 mm; mesoplankton-fed, 9.907 ± 0.732 mm).

There was no significant difference in the wet weights of each diet fed the lobsters. The average wet weights of the diets were 0.408 ± 0.095 g for the mesoplankton; 0.364 ± 0.108 g for the meso/microplankton combination diet; and 0.391 ± 0.072 g for the brine shrimp diets. The mesoplankton diet consisted predominantly of *Acartia* copepods, barnacle nauplii, pagurid shrimp zoea, invertebrate eggs, brachyuran crab zoea, foraminifera, centric and pennate diatoms, and marine algae, with occasional instances of ascidian tadpoles, barnacle exoskeletons, fish eggs and young, amphipods, hydroids, brachyuran crab prezoea,

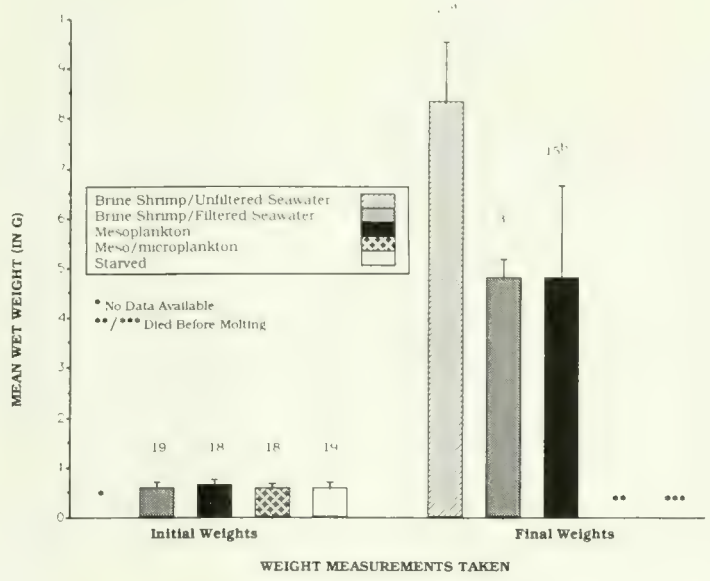

Figure 3

Initial (Stage V) and final (Stage IX) mean wet weight measurements (g) for lobsters on the five diets: brine shrimp in unfiltered seawater, brine shrimp in filtered seawater, mesoplankton (95–1000 μm) in filtered seawater, meso/microplankton combination (25–95 μm), and starved. Bars indicate standard deviation values. (a) Two lobsters missed in weighing schedule. (b) One lobster missed in weighing schedule.

caridean shrimp zoea, *Centropages* and *Calanus* copepods, dinoflagellates, and juvenile nemertea. The meso/microplankton combination diet typically consisted of centric and pennate diatoms with occasional instances of fragments of marine algae and crustaceans.

Discussion

The results clearly indicate that early juvenile American lobsters are not capable of extending survival on a diet consisting mostly of diatoms, despite their common presence in stomach content analyses (Herrick 1895, Williams 1907, Herrick 1911). Larger planktonic organisms are required for survival and growth. This result is not entirely surprising even though Lavalli and Barshaw (1989) showed that post-larval and early juvenile (Stage V) American lobsters could remove particles from the water down to a size of at least 70 μm. Other crustaceans fed on phytoplankton can gain some nutrients and extend their survival in periods of low

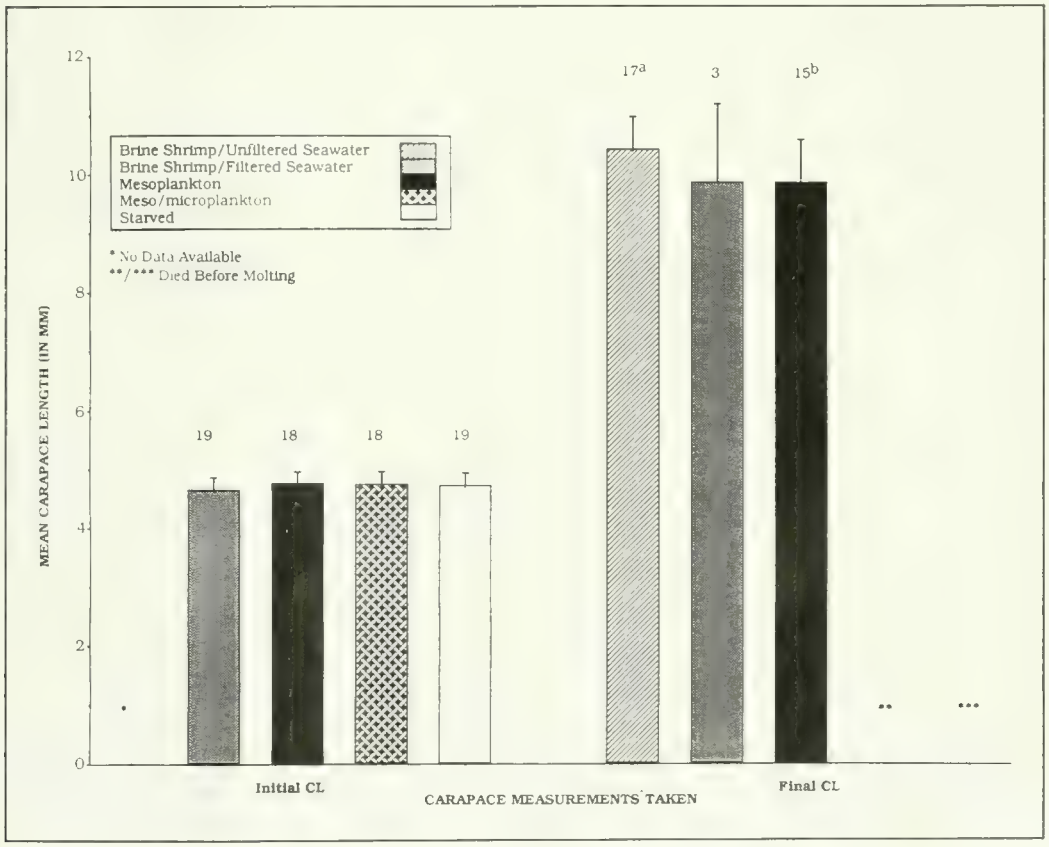

Figure 4

Initial (Stage V) and final (Stage IX) mean carapace length measurements (mm) for lobsters on the five diets: brine shrimp in unfiltered seawater, brine shrimp in filtered seawater, mesoplankton (95–1000 μm) in filtered seawater, meso/microplankton combination, and starved. Bars indicate standard deviation values. (a) Two lobsters missed in carapace-length measuring schedule. (b) One lobster missed in carapace-length measuring schedule.

food abundance, but this type of diet does not support molting or growth (McConaugha 1985). Post-larval lobsters are known to contain diatoms and other algae in their guts (Herrick 1895, Williams 1907, Herrick 1911) which suggests some nutritional role for these items, but one not fully understood nor clarified by this experiment. The smaller planktonic organisms in the meso/microplankton combination diet may not have been present in sufficient numbers to make up for the small amount of nutrients derived. Because the meso/microplankton diet consisted mostly of diatoms which have a high content of silicon-based ash, it is likely that this diet had a greater percentage of non-digestible fiber or bulk than that in the mesoplankton or brine shrimp diets (John Castell, Dep. Fish. & Oceans, Halifax, N.S., Canada B3J 2S7, pers. commun., May 1990). Furthermore, these smaller organisms may have been more easily flushed out of the containers when the water flow resumed.

The results presented here also clearly support those of Barshaw (1989) and Daniel et al. (1985) in terms of postlarval and early-juvenile lobsters being capable of surviving on mesoplankton, and in demonstrating high survival among the brine shrimp-fed (in filtered seawater) and mesoplankton-fed groups through Stage VI. These studies differ, however, in that Barshaw (1989) found molt delays in her plankton-fed group between Stages V and VI, whereas no molt delays were found in this study until Stage VIII. Barshaw's lobsters also took longer to molt into Stage VI (34 days for the plankton-fed lobsters and 23 days for the brine shrimp-fed lobsters) than did the lobsters in this experiment (10 and 11 days for the same groups), indicating that they were not receiving enough food and thus took longer to build up the reserves to molt. In addition, both Daniel et al. (1985) and Barshaw (1989) found that lobsters fed on frozen brine shrimp in filtered seawater were significantly larger than the filtrate-fed or plankton-fed lobsters. This study found no such difference between the similarly treated groups.

The differences between the two groups of lobsters fed on brine shrimp diets were striking. Lobsters fed brine shrimp in the filtered seawater had pale blue coloration and poor survival, with the majority of deaths occurring during molting. However, this difference in survival was not present until after Stage VI where Barshaw's (1989) experiment ended. Similar drops in survival of brine shrimp-fed lobsters in filtered seawater after Stage VI have been observed by Colleen Boggs (Edgerton Res. Lab. [in collaboration with the Kravitz Lab., Harvard Medical School], New England Aquarium, Boston 02110, pers. commun., summer 1990). Certain strains of brine shrimp promote better growth than others (McConaugha 1985), and the success of one strain versus another is linked to its fatty acid content (Fujita et al. 1980), the presence of which is extremely important for the survival of postlarval and early-juvenile American lobsters (D'Abramo et al. 1981). The San Francisco Bay brand used in this experiment is intermediate in lipid content (McConaugha 1985), but even different lots of the same strain of brine shrimp are known to be highly variable in quality (Eagles et al. 1984, 1986). Thus, whatever nutritional component was lacking in the lot of the brine shrimp used in this experiment was compensated by the planktonic organisms entering through the ambient water supply, since the brine shrimp-fed group of lobsters in unfiltered seawater showed high survival, a greater weight increase compared with those in filtered seawater, and wild-type coloration. What is particularly interesting, though, is that while the lobsters fed brine shrimp in unfiltered seawater were nearly twice as heavy at Stage IX as both those fed brine shrimp in filtered seawater and mesoplankton, there was no significant difference at Stage IX between any of these groups in terms of carapace lengths. Weight, therefore, might be a more important index of growth in early-juvenile lobsters. The carapace lengths achieved by the three surviving groups of lobsters at Stage IX were shorter than those predicted by calculations of Hudon (1987) from early juveniles captured in the field. This contradiction may have resulted from the lobsters used in this experiment being hatchery- and laboratory-reared and thus being typically smaller than wild lobsters at Stage V (pers. observ.).

The difference in weights at Stage IX between lobsters fed brine shrimp in unfiltered seawater and those fed mesoplankton indicates that growth (as well as survival) might be significantly enhanced if the lobsters have access to both a planktonic diet and a diet of small benthic organisms. Andrea (1975) demonstrated that lobster larvae (Stages I–IV) fed frozen copepods or frozen amphipods had significantly higher survival rates than those fed frozen brine shrimp. Furthermore, those larvae fed live copepods had higher survival than those fed both live and frozen adult brine shrimp when held under the same rearing conditions. Andrea's data also showed that the increase in carapace length and the gain in weight by lobsters fed diets of live copepods were comparable to the increases found in lobsters fed live brine shrimp.

Evidence to date indicates that early juveniles are found in shallow subtidal areas (Cooper and Uzmann 1980, Hudon 1987, Able et al. 1988, Wahle 1990) where they would have access to suprabenthic plankton and epiplankton (Wieser 1960, Cornet et al. 1983) as well as surface plankton that vertically migrate in response to light/dark conditions (Hardy 1970). They would also have access to the many benthic organisms found in subtidal areas (Orth 1973, Reise 1977). In support of

this hypothesis, postlarvae and early juveniles in laboratory settings have been observed to lunge out of their burrows to grab at food (amphipods) passing by (Berrill 1974 with *H. gammarus*; Barshaw and Bryant-Rich 1988) or to stalk swimming amphipods (Good et al. 1982). Also, Crnkovic (1968) suggested that the creation of new openings in existing *Nephrops norvegicus* burrows may be linked to searching for food within the sediment.

The intermolt periods, with the exception of that for the mesoplankton-fed group between Stages VIII and IX, were consistent with or shorter than previous studies at the same average temperature (19°C) (Templeman 1948, as reported in Wilder 1953) and were close to the values predicted by Hudon (1987) for the same stages. These results show that early-juvenile lobsters fed on mesoplankton are able to capture it effectively enough to keep pace with the brine shrimp-fed lobsters in terms of intermolt periods until Stage VIII. At that time, the mesoplankton-fed lobsters spend nearly twice as much time in intermolt than either of the brine shrimp-fed groups. This result could be indicative of one of three conditions or some combination of all of them: (1) Either the lobsters became less efficient at capturing the plankton, (2) the planktonic organisms were not present in sufficient numbers in this study to compete with a brine shrimp diet at later stages, or (3) dietary requirements change with later molt stages.

In support of the first hypothesis is the fact that the claws of the postlarvae are small and symmetrical prior to Stage VIII. The claws slowly develop into the crusher and seizer claws during the early-juvenile stages; concomitant with this gradual development is a change in the posture of the lobster from one that is completely defensive (withdrawing or tail-flipping) to one that is more aggressive (Lang et al. 1977), and a change in the muscle fiber pattern and innervation of the two types of claws (Govind 1984). At Stage VIII the claw asymmetry is well established and the fiber composition and innervation are nearly the same as that found in the adult (Govind and Pearce 1986). These changes may indicate a shift in the feeding strategies used by the lobster, where capture of small benthic organisms becomes more important than the capture of planktonic organisms at or near Stage VIII.

As for the second hypothesis, Bordner and Conklin (1981) determined that older juvenile lobsters could consume up to 10% of their body weight per day. During this entire experiment, each group of lobsters was fed more than 10% of their body weight per day. Therefore, it seems unlikely that the later stages of lobsters were underfed on the mesoplankton diet. Finally, dietary requirements might indeed change as the lobster becomes more able to defend itself and thereby forage, and as the claws develop the ability to crush small molluscs; however, this experiment was not designed to answer such a question.

In conclusion, the results from this experiment contradict those of Barshaw (1989) and Daniel et al. (1985) in that they show no difference in growth and survival of early-juvenile lobsters (Stages V and VI) fed on a diet of mesoplankton versus a diet of frozen brine shrimp in filtered seawater. Stage VI–VIII lobsters are able to survive and grow on planktonic diets, but after Stage VIII they experience molt delays when compared with lobsters fed frozen brine shrimp diets. Despite this delay, the mesoplankton diet allows the early juveniles the opportunity to reach the predicted (Hudon 1987) winter stages of Stage VI (for late-fall settlers) to IX or X (for August settlers) without the need for other benthic food. Diets composed of smaller members of the mesoplankton plus microplankton do not provide sufficient nutrition to support survival in periods of low food abundance.

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Diel Sampling of Migratory Juvenile Salmonids in the Columbia River Estuary

Richard D. Ledgerwood

Coastal Zone and Estuarine Studies Division
Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East, Seattle, Washington 98112-2097

Frank P. Thrower

Auke Bay Laboratory, Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 210155, Auke Bay, Alaska 99821

Earl M. Dawley

Coastal Zone and Estuarine Studies Division
Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East, Seattle, Washington 98112-2097

Abstract. – Beach and purse seine catches at Jones Beach, River kilometer 75, were used to examine diel movement patterns of juvenile chinook salmon *Oncorhynchus tshawytscha*, coho salmon *O. kisutch*, and steelhead *O. mykiss* as they migrated downstream in the Columbia River estuary. The patterns were monitored during five 24-hour periods in 1978, 1979, and 1980, and compared with patterns obtained from extensive morning-hour sampling conducted during 1979–83. Diel catch patterns were generally consistent among the sampling periods and there was reasonable agreement with morning-hour sampling. However, diel movement was different than that reported for salmonids in other river systems and in other locations in the Columbia River. The times and lateral position of greatest downstream movement which provided the largest catches of salmonid juveniles were as follows: sunrise to early afternoon nearshore for subyearling chinook salmon, sunrise to early afternoon midriver for yearling chinook salmon, midmorning to early evening nearshore and sunrise to early afternoon midriver for coho salmon, and noon to early evening midriver for steelhead. Decreased movement during darkness was apparent for all salmonids. No relationship between tidal cycle and catch was evident from either beach or purse seine sampling.

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Successful and cost-effective timing and survival studies for juvenile salmon and steelhead are dependent on understanding migratory behavior as well as sampling effectiveness. Literature regarding the migratory behavior of juvenile Pacific salmon *Oncorhynchus* spp. and steelhead *O. mykiss* indicates a wide variation in diel movement patterns, from greatest movement during daylight hours (Sims et al. 1976) to greatest movement at night (Smith et al. 1968) (see also Table 1). Catches used for the reported observations were obtained using an assortment of sampling equipment in large and small rivers and reservoirs during a range of turbidity conditions. Juveniles captured varied in life stage from emergent fry to migrating smolt. It was difficult to determine from some of the literature whether the greatest catches represented increased fish movement or times of greatest susceptibility to sampling equipment.

Personnel of the National Marine Fisheries Service conducted a sampling program at Jones Beach, Columbia River, kilometer (Rkm) 75, to examine diel movement patterns of juvenile chinook salmon *O. tshawytscha*, coho salmon *O. kisutch*, and steelhead in the upper Columbia River estuary. The objective was to establish the optimum time of day and lateral location for the most effective sampling of these fish during the peak of the spring migration. Also, this program was to provide data to compare with previous sampling results at Jones Beach which indicated midriver orientation of yearling fish, shore orientation of subyearling fish, and substantially decreased movement of shore-oriented migrants at night (Dawley et al. 1986).

Methods

Diel migration patterns were monitored using beach and/or purse seines during five 24-hour periods: 18–19 May 1978, 14–15 June 1978, and 14–15 May 1980 for beach seine; and 10–11 May 1979, 23–24 May 1979, and 14–15 May 1980 for purse seine. Sampling dates were based on peaks of juvenile salmonid migrations recorded in other years (1966–83) at Jones Beach (Dawley et al. 1986).

Purse seining was conducted midriver from the north edge of the ship channel toward Puget Island; beach

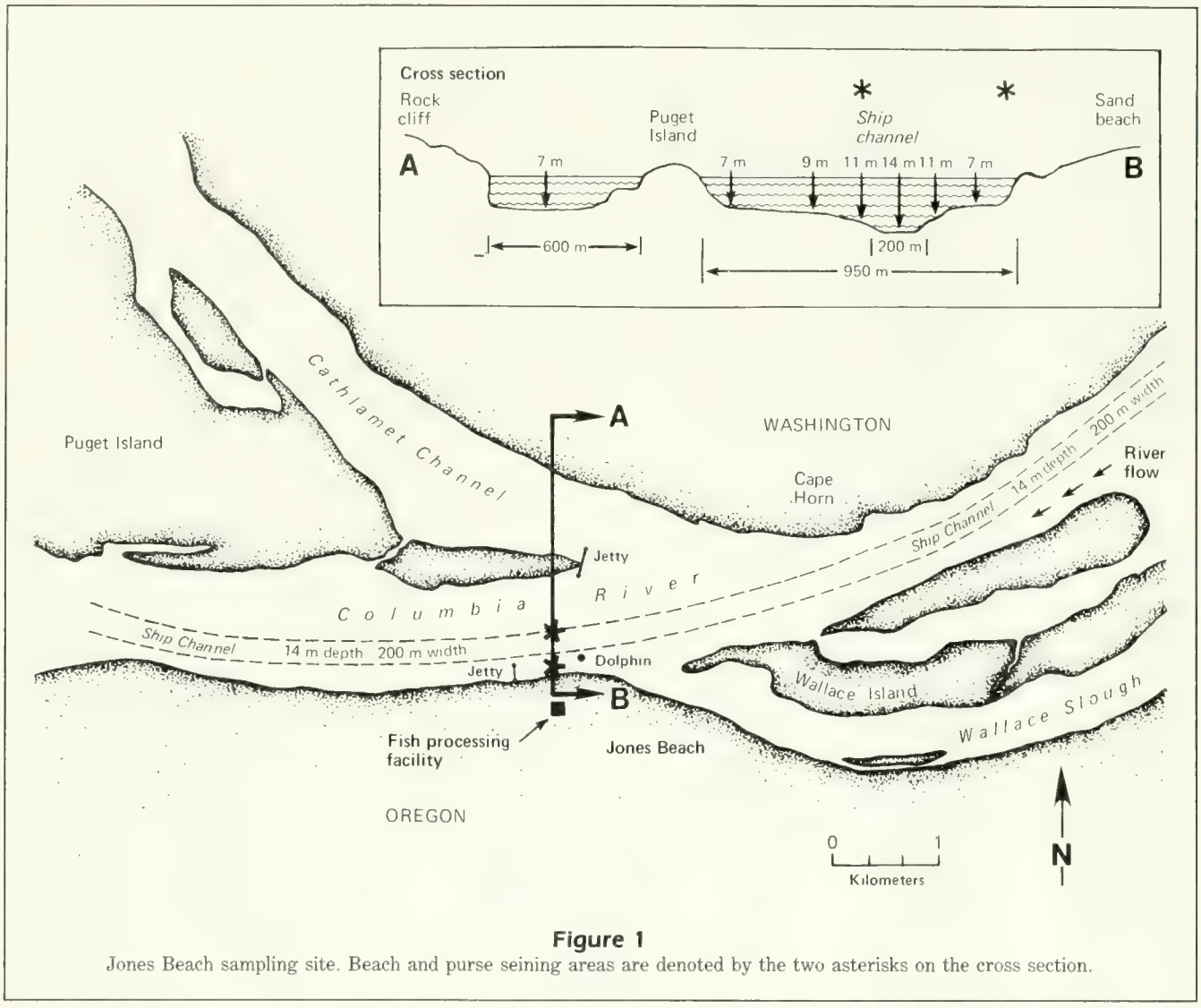

Figure 1

Jones Beach sampling site. Beach and purse seining areas are denoted by the two asterisks on the cross section.

seining was on the south shoreline, lateral to the purse seine site (Fig. 1).

Conditions of the Columbia River were different during each sampling period. River flows ranged from 6800 to 7600 m^3/second (U.S. Army Corps of Engineers 1978–80). Turbidity and water temperatures ranged from 5 to 11 Jackson Turbidity Units and 12° to 17°C, respectively. Tides at Jones Beach are semidiurnal (~7 hours of ebb and 4.5 hours of flood current); flow reversal occurs during flood tides throughout most of the year. River flows in the range of 5000–12,000 m^3/second generally occur during the period May through mid-July, and flood tide effects are diminished at these high flows.

Captured salmonids were anesthetized, identified to species, and enumerated (Dawley et al. 1985). Subyearling and yearling chinook salmon were separated on the basis of fork length; separation points were determined from the bimodal curves of length frequency. Verification of age from marked fish of known age (4.8–6.5% of catch) showed about 4% error in separation. All captured fish were either held in tanks onshore until sampling was complete and then released or transported downstream from the sampling area and released.

Beach seining

The beach seine was 95 m long by 5 m deep with 1–2 cm (stretch) webbing (Sims and Johnsen 1974). The net was fished downstream regardless of tidal influence. An anchor was used to secure one end of the net onshore and the opposite end, containing the bunt, was towed upstream at the 1-m depth contour, then arched

downstream and back to shore. The effective fishing depth of the net was 2–3 m in water up to 6 m deep. The net was pulled onto the beach which crowded the fish into the bunt for capture. Completion of each set required about 25 minutes; sets were made at 45-minute intervals.

Catch data from the first two or three seine sets on the first morning of each sampling period were not used for analysis of diel movement because some salmonids probably resided in the sampling area overnight, and the initial sets were used to clear the sampling site of those residents. Of the beach seine sets in each 24-hour period, 34% (11 of 32) were made during darkness and 66% (21 of 32) during daylight.

Purse seining

The purse seine was 206 m long by 11 m deep with 1–2 cm (stretch) webbing (Durkin and Park 1967). A depressor weight was used during the pursing operation to increase the effective fishing depth to about 6 m. The vessels used were a 10-m pontoon barge powered by outboard engines and an outboard- motored seine skiff; lights were mounted on the barge for night operation. A depth finder, a compass, and channel markers were used to locate the sampling site.

The seine was set near midriver in water 9–14 m deep, and towed upstream at constant power in a "U" configuration (Dawley et al. 1985). After 5 minutes, the ends of the net were brought together and the net bottom was closed (pursed) and hauled aboard the barge with a boom and hydraulic capstan. Then the cork line and webbing were retrieved and the catch was placed in 75-L containers supplied with circulating river water. Completion of each set required about 40 minutes; sets were made at 90-minute intervals. About 31% (5 of 16) of the purse seine sets were made during darkness and 69% (11 of 16) during daylight.

Data analysis

Each set represented one time interval within the 24-hour sampling period. Twice as many beach seine sets were made in each 24-hour period as purse seine sets; consequently, time intervals are one-half those for the purse seine. The catch per set (CPS) interval was calculated in terms of the percentage of the total 24-hour catch by species and stock. An overall percent CPS was calculated for each seine type by averaging interval values from the three appropriate sampling dates.

Diel catch data for each species were compared graphically and with linear regression to corresponding tidal heights at Jones Beach.

Results

During 14–15 May 1980, the only period we sampled with both beach and purse seines, the beach seine accounted for 79% of the total catch of subyearling chinook salmon (predominately fall race) (Van Hyning 1973), while the purse seine produced the largest catches of yearling fish: 92% of the yearling chinook salmon (predominately spring race); 82% of the coho salmon; 100% of the sockeye salmon *O. nerka*; and 97% of the steelhead. Daylight sampling in previous years produced similar beach seine to purse seine catch ratios (Dawley et al. 1986).

Examination of catch data indicated there was no apparent relationship to tidal variations for any species during any sampling period; correlation coefficients ranged from −0.51 to 0.14. Catch/tidal data are available upon request. Dawley et al. (1986) also observed a lack of correlation between tidal cycles and beach seine catches of subyearling chinook salmon from the Columbia River estuary.

Subyearling chinook salmon

Beach seine catches of subyearling chinook salmon (13,513 fish) peaked during the interval about 1.5 hours after sunrise (6.9% CPS) followed by steady catches during the daylight intervals, each near 4.0% CPS. About 1.5 hours before sunset, a second, smaller peak was observed in two intervals (CPS of 5.2% each), followed by a sharp and continued decrease with darkness through the night intervals (average CPS = 0.9%). The night catch was 10.2% (3.8 SD) of the total catch for a 24-hour period. Catches increased again about 45 minutes before sunrise (Fig. 2A).

Purse seine catches of subyearling chinook salmon (1461 fish) increased just before sunrise and decreased throughout the day (Fig. 2B). Again, only 10% (1.7 SD) of the total purse seine catch was at night.

Coho salmon

About 21% of the yearling coho salmon captured were from beach seining (1092 by beach seine and 3990 by purse seine). The June 1978 sampling period produced only 17 fish and was not included in the assessment of movement behavior. Beach seine catches in daylight were low until about 1000 hours then generally increased, with large fluctuations between intervals, to a peak at about 1430 hours (10.7% CPS) (Fig. 2C). In the late afternoon and evening, catches generally decreased with large fluctuations between intervals. The CPS dropped at dusk to 2.5% followed by lower catches during darkness. The night catch averaged

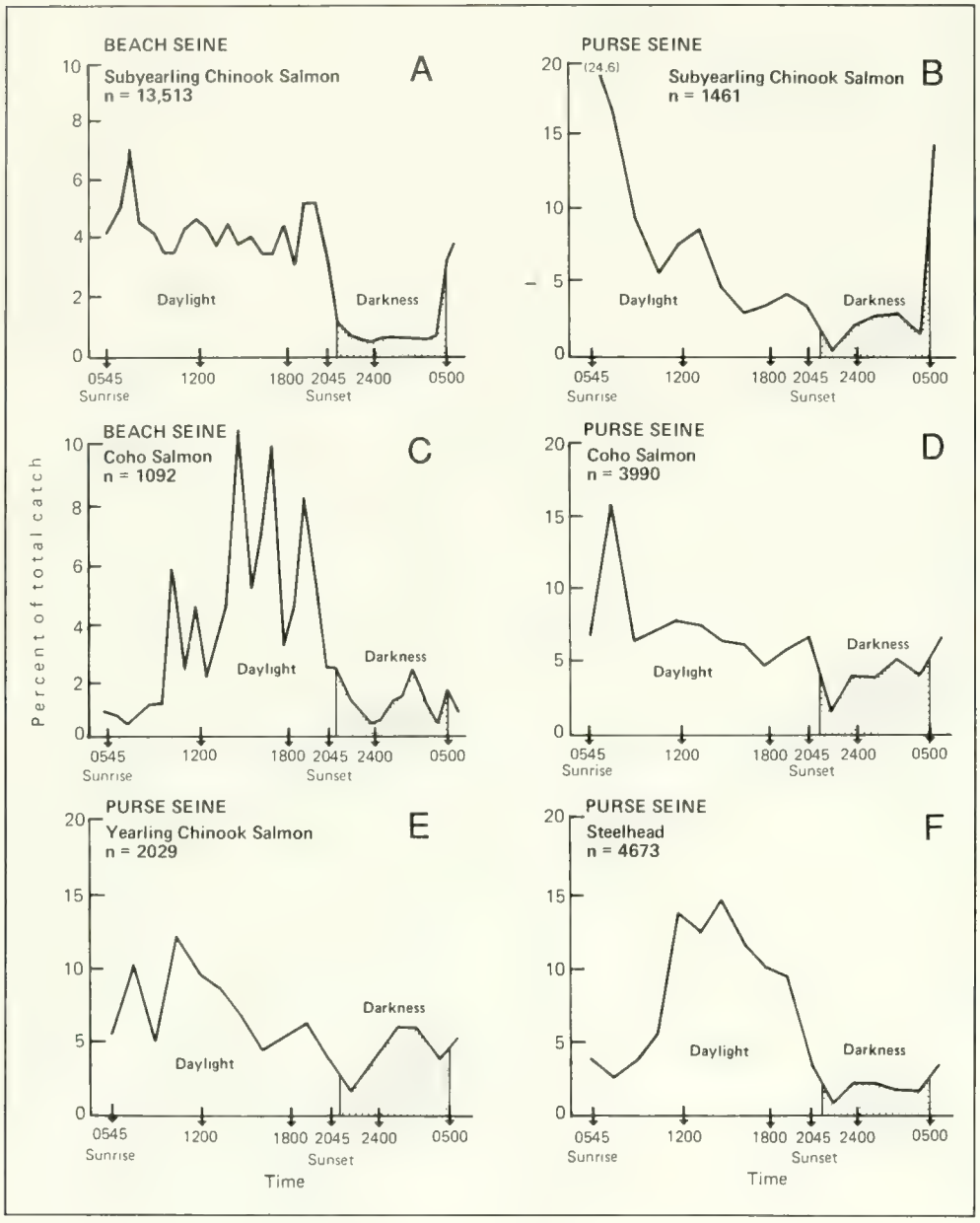

Figure 2
Diel catch patterns for chinook salmon, coho salmon, and steelhead from beach and purse seine sampling at Jones Beach, 1978–80 (samples combined and averaged).

13.7% of the total catch for the two 24-hour sampling periods.

Purse seine catches peaked during the interval about 1.5 hours after daylight (15.8% CPS) and remained near 6.5% CPS throughout the daylight intervals the (Fig. 2D). Catches decreased in the night intervals to an average 3.7% CPS; 18.5% (4.6 SD) of the CPS was obtained during darkness.

Yearling chinook salmon

The majority of yearling chinook salmon migrated mid-river; purse seine catches totaled 2029 fish compared with 113 from the beach seine. The peak catch with the purse seine was during the interval 0946 to 1115 hours (12.3% CPS). Overall, 46% of the total catch was taken in 31% of the sets (1.5 hours after sunrise to about 1330 hours) (Fig. 2E). Purse seine catches were smallest from dusk to midnight (average 3.2% CPS), with larger catches occurring during the remainder of the night intervals (average 5.4% CPS). The night catch was 21.1% (7.0 SD) of the total purse seine catch for a 24-hour period.

Sockeye salmon

Sockeye salmon juveniles were caught only in the purse seine (222 fish), with 15% (6.3 SD) captured at

night. An insufficient number of fish were captured to allow a more detailed analysis of the diel migration pattern.

Steelhead

Over 98% of the juvenile steelhead were caught by purse seine (4673 by purse seine and 74 by beach seine). Purse seine catches were moderate in the four intervals after sunrise (average 4% CPS), peaked at the interval from 1416 to 1545 hours (14.6% CPS), decreased at dusk, and remained low throughout the night intervals (average 1.7% CPS) (Fig. 2F). The night catch was 8.7% (1.0 SD) of the total catch for a 24-hour period.

Discussion

Catch data from our beach and purse seines appear to represent movement and position of juvenile salmonids during their migration through the upper Columbia River estuary. Catches of subyearling chinook salmon at both purse and beach seining sites indicate a substantially decreased migration during darkness. Beach (nearshore) and purse (midriver) seine catches of coho salmon indicate a fairly uniform migration throughout the daylight period. Data obtained for yearling chinook salmon, sockeye salmon, and steelhead indicate a midriver orientation with decreased migration during darkness. Other researchers have reported different diel movement patterns, but conditions, equipment, and life stages of the fish sampled are so variable that direct comparison between experiments is difficult (Table 1).

Table 1

Summary of diel observations of juvenile chinook and coho salmon and steelhead in various Pacific Northwest and Alaska river systems.

Environment	Life stage	Location	Method	Pertinent observations of movement behavior	Source
Yearling chinook salmon					
River	Smolt	Central Ferry Bridge (Snake R.)	Fyke net	Largest catches between 0300 and 0600 h, smallest catches between 0600 and 1200 h. Largest catches from shoreline areas during low and medium river flow, and midriver areas during high flow. Catches uniform in number from surface to bottom.	Mains and Smith 1964
River	Smolt	Byer's Landing (mid-Columbia R.)	Fyke net	Largest catches (70%) between 1800 and 0600 h. Largest catches in shoreline areas. Largest catches in surface water (0.8 m).	Mains and Smith 1964
Reservoir	Smolt	John Day (Columbia R.)	Purse seine	Largest catches during daylight (0700–2100 h).	Sims et al. 1976
Reservoir	Smolt	Lower Monumental (Snake R.)	Monofilament gillnet	Largest catches at night; 92% of total catch. Catches in the upper 7.3 m were 5 during the day and 109 at night, and catches below 7.3 m increased from 6 during the day to 19 at night. Largest catches in central portion of reservoir, day and night.	Smith 1974
Reservoir	Smolt and fry	Mayfield (Cowlitz R.)	Floating fish trap	Largest catches (82% of total obtained between 2000 and 0800 h.	Allen 1965
Reservoir	Fingerling and fry	Upper Mayfield (Cowlitz R.)	Trawl and gillnet	Largest catches during darkness or periods of high turbidity (trawl). Largest catches (87%) in upper 7.3 m. Movement of fish not strongly downstream.	Smith et al. 1968
Reservoir	Smolt and fingerling	North Fork (Clackamas R.)	Gillnet	Largest catches during darkness near surface (0–5 m) over deep water (15 m).	Korn et al. 1967
Reservoir	Smolt	Rocky Reach (Columbia R.)	Sonar	Highest movement between dusk and dawn.	Leman 1978

Table 1 (continued)

Environment	Life stage	Location	Method	Pertinent observations of movement behavior	Source
Yearling chinook salmon (continued)					
Dam	Smolt	John Day (Columbia R.)	Dip net and airlift pump	Largest catches (92% of total) between dusk and dawn (8.5-h period). Turbine intake, 20 m below surface.	Sims et al. 1976 Sims and Ossiander 1981
Dam	Smolt	The Dalles (Columbia R.)	Fyke net in turbine intake	Largest catches (94%) at night (1900–0700 h). Largest catches (75% of total) from upper third of intakes (top of turbine intake, 6 m below surface).	Long 1968
			Dip net in gatewell	Largest catches during daylight (0700–2100 h) with only 11% of total caught in darkness (8.5-h period).	Sims et al. 1976 Nichols 1979
Dam	Smolt	The Dalles (Columbia R.)	Fyke net in sluiceway	Largest catches in daylight (0800–1400 h) with few fish after dark; 3-ft deep surface flow over sluiceway gate. Largest catches near dusk (1700–2200 h) with few fish at other periods; 2-ft deep surface flow over sluiceway gate.	Nichols 1979
Subyearling chinook salmon					
Estuary	Smolt	Puget Island and Jones Beach (Columbia R. estuary)	Beach seine	90% of catch from daylight sets (0600–2100 h). Largest catches during early morning and at dusk.	Dawley et al. 1986
River	Fingerling and fry	Sixes R. (Oregon R.)	Traps	Both emergence of fry from the gravel and downstream migration of fry and fingerling primarily during darkness.	Reimers 1973
Reservoir	Smolt	John Day (Columbia R.)	Purse seine	Largest catches during daylight (0700–2100 h).	Sims et al. 1976
Dam	Smolt	John Day (Columbia R.)	Dip net and airlift pump in gatewell	Largest catches (88% of total) between dusk and dawn. Turbine intake, 20 m below surface.	Sims et al. 1976 Sims and Ossiander 1981
Dam	Smolt	The Dalles (Columbia R.)	Fyke net in turbine intake	Largest catches (67%) at night (1900–0700 h). Largest catches (49% of total) from upper third of water column (4.4 m) entering the intakes (top of turbine intake, 6 m below surface).	Long 1968
			Dip net in gatewell	Largest catches during daylight (0700–2100 h) with 10% of total caught in darkness (8.5-h period). Turbine intake, 6 m below surface.	Sims et al. 1976 Nichols and Ransom 1980
Dam	Smolt	The Dalles (Columbia R.)	Fyke net in sluiceway	Largest catches in daylight (0600–0700 and 1400–2100 h) with few fish after dark; 3-ft deep surface flow over sluiceway gate.	Nichols and Ransom 1980
Coho salmon					
Estuary	Smolt	Columbia R.	Purse seine	Largest catches at midday (1000–1400 h).	Durkin 1982
River	Smolt	Minter Creek (Puget Sound)	Trap	Largest catches at dawn and dusk.	Salo and Bayliff 1958
River	Smolt	Taku R. (S.E. Alaska)	Scoop trap	Largest catches at dawn and dusk.	Meehan and Siniff 1962
Reservoir	Smolt	Brownlee (Snake R.)	Fyke net	Largest catches at dawn and dusk.	Monan et al. 1969
Reservoir	Smolt	John Day (Columbia R.)	Purse seine	Largest catches during daylight (0700–2100 h).	Sims et al. 1976

Table 1 (continued)

Environment	Life stage	Location	Method	Pertinent observations of movement behavior	Source
Coho salmon (continued)					
Reservoir	Smolt and fingerling	North Fork (Clackamas R.)	Gillnet	Largest catches at dawn and dusk; near surface during darkness and deeper during daylight.	Korn et al. 1967
Reservoir	Smolt and fingerling	Round Butte (Deschutes R.)	Gillnet	Few fish captured during daylight during any season. During spring migration period, smolts captured principally near surface (0–3.7 m).	Korn et al. 1967
Reservoir	Fingerling and fry	Upper Mayfield (Cowlitz R.)	Trawl and gillnet	Largest catches during darkness or periods of high turbidity (trawl). Largest catches (87%) near surface (0–7.3 m). Movement of fish not strongly downstream.	Smith et al. 1968
Dam	Smolt	John Day (Columbia R.)	Dip net in gatewell of dam	Largest catches during darkness (2100–0700 h). Turbine intake, 20 m below surface.	Sims et al. 1976
Dam	Smolt	The Dalles (Columbia R.)	Dip net in gatewell of dam	Largest catches during daylight (0700–2100 h). Turbine intake, 6 m below surface	Sims et al. 1976
Dam	Smolt	The Dalles (Columbia R.)	Fyke net in sluiceway	Largest catches in daylight (0800–1400 h) with few fish after dark; 3-ft deep surface flow over sluiceway gate. Largest catches near dusk (1700–2200 h) with few fish at other periods; 2-ft deep surface flow over sluiceway gate.	Nichols 1979
Steelhead					
Reservoir	Smolt	John Day (Columbia R.)	Purse seine	Largest catches during daylight (0700–2100 h).	Sims et al. 1976
Reservoir	Smolt	Lower Monumental (Snake R.)	Monofilament gillnet	Largest catches at night; 76% of daily total. Catches in the upper 7.3 m increased from 146 during the day to 396 at night and catches below 7.3 m from 56 during the day to 420 at night. Uniform distribution across the reservoir day and night.	Smith 1974
Reservoir	Smolt and fry	Mayfield (Cowlitz R.)	Floating fish trap	Largest catches (82% of total) obtained between 2000 and 0800 h.	Allen 1965
Reservoir	Fingerling and fry	Upper Mayfield (Cowlitz R.)	Trawl and gillnet	Largest catches during darkness or periods of high turbidity (trawl). Largest catches (87%) in upper 7.3 m. Movement of fish not strongly downstream.	Smith et al. 1968
Reservoir	Smolt and fingerling	North Fork (Clackamas R.)	Gillnet	Largest catches (few fish) during darkness near surface over deep water.	Korn et al. 1967
Dam	Smolt	John Day (Columbia R.)	Dip net and airlift pump in gatewell of dam	Largest catches (77% of total) between dusk and dawn (8.5 h period). Turbine intake, 20 m below surface.	Sims et al. 1976
Dam	Smolt	The Dalles (Columbia R.)	Fyke net in turbine intake	Largest catches (85%) at night (1900–0700 h). Largest catches (72% of total) from the upper third of the water column (4.4 m) entering the intakes (top of turbine intake, 6 m below surface).	Long 1968

Table 1 (continued)

Environment	Life stage	Location	Method	Pertinent observations of movement behavior	Source
Steelhead (continued)					
Dam	Smolt	The Dalles (Columbia R.)	Fyke net in turbine intake	Largest catches during daylight with only 29% of total caught in darkness (8.5 h period). Turbine intake, 6 m below surface.	Sims et al. 1976
Dam	Smolt	The Dalles (Columbian R.)	Fyke net in sluiceway	Largest catches in daylight (0800–1400 h) with few fish after dark; 3-ft deep surface flow over sluiceway gate. Largest catches near dusk (1700–2200 h) with few fish at other periods; 2-ft deep surface flow over sluiceway gate.	Nichols 1979

Variability of catch between sets and sampling periods was higher for yearling chinook salmon than for other salmonids. The origin of marked fish varied substantially among the three purse-seine sampling periods (Table 2). The largest portions of the catch originated in the Willamette, mid-Columbia, and Snake Rivers for the first, second, and third sampling periods, respectively. Stock differences and changes in abundance among stocks during the diel sampling periods may have caused the higher variability in the catch.

We found reasonable agreement among the diel catch patterns reported here and those from extensive morning sampling (2615 sets) at Jones Beach in May and June 1979–83 (Dawley et al. 1986) (Fig. 3). A noteworthy exception was that beach seine catches near sunrise were lower during the diel study because sets were made before sunrise to remove fish which resided in the area overnight.

It is generally agreed that net avoidance is probably greatest in daylight; therefore, decreased net catches at night should represent decreased fish abundance in the water sampled. It seems unlikely that decreased catches at Jones Beach during darkness were caused by surface- or midwater-oriented juveniles maintaining their position against current velocities up to 5 km/hour. Data obtained at Jones Beach by Dawley et al. (1986) showed that marked subyearling chinook salmon released into the shoreline sampling area at night were recaptured at a much higher rate than marked fish released during daylight (30.6 vs. 8.0%). Because midriver-oriented yearling fish do not appear in shoreline areas at Jones Beach during darkness, they probably hold near the bottom,

Table 2

Origin of marked yearling chinook salmon captured by purse seine during diel sampling, 1979 and 1980.

	Sampling dates		
Origin	10–11 May 1979	23–24 May 1979	14–15 May 1980
	% of marks		
Snake River	7	19	60
mid-Columbia River	13	47	40
Transported and released downstream from Bonneville Dam	33	28	0
Willamette River	40	0	0
Lower Columbia River	7	6	0

Table 3

Measured movement rates of juvenile salmonids and water velocities in a 155-km reach of the Columbia River between Bonneville Dam and Jones Beach at two volumes of river flow.

River flows (1000 m^3/s)	Water velocity (km/h)[b]	Movement rates (km/h)[a]			
		Chinook salmon		Coho salmon	Steelhead
		Subyearling	Yearling		
8.1 ± 0.5	4.8	0.9	0.8	1.4	3.2
11.3 ± 0.5	5.0	1.0	—	0.9	1.7

[a] Zero to nine marked groups were available for each calculation of average movement rate at these designated river flows (Dawley et al. 1986).
[b] From Blahm (1974).

particularly in deep areas of low current velocity. This premise is supported by studies on water velocity (Blahm 1974) and the movement rates of marked juvenile salmon released below Bonneville Dam and recovered at Jones Beach (Dawley et al. 1986) (Table 3). In all cases, fish migration speeds from release site to capture in the estuary were less than water velocity (Dawley et al. 1986).

In conclusion, the most appropriate times and locations for sampling to attain maximum CPSs are as follows: Subyearling chinook salmon, sunrise to early afternoon nearshore; yearling chinook salmon, sunrise to early afternoon midriver; yearling coho salmon, midmorning to early evening nearshore and sunrise to early afternoon midriver; juvenile steelhead, noon to early evening midriver.

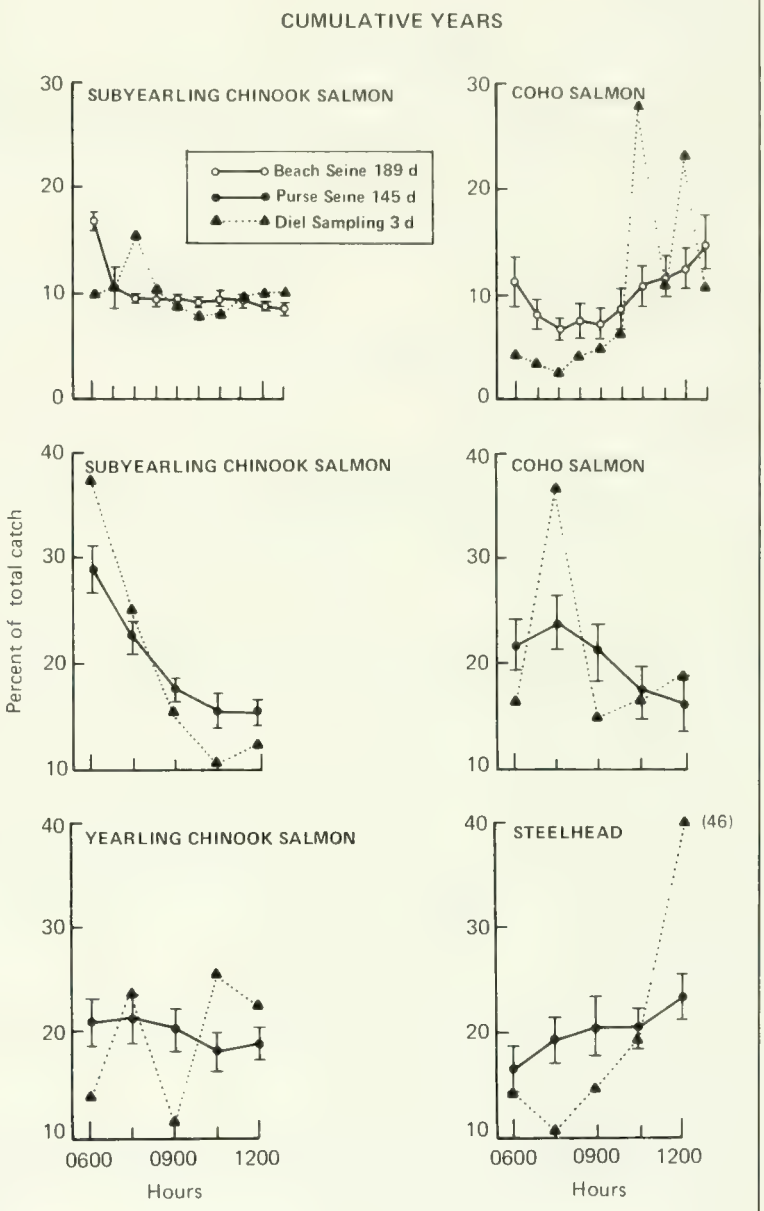

Figure 3

Percent total catch of juvenile salmonids during morning hour sampling at Jones Beach, Columbia River (1979–83) compared with diel sampling results (mean value per time interval and 95% confidence limits); d = total number of sampling days used for each estimate.

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Fishery Characteristics, Growth, and Movements of the Spiny Lobster *Panulirus argus* in Bahia de la Ascension, Mexico

Enrique Lozano-Alvarez
Patricia Briones-Fourzan

Universidad Nacional Autonoma de Mexico
Instituto de Ciencias del Mar y Limnologia, Estacion "Puerto Morelos"
P.O. Box 1152, Cancun, Q.R., 77500 Mexico

Bruce F. Phillips

Commonwealth Scientific and Industrial Research Organization (CSIRO)
Marine Laboratory, P.O. Box 20, North Beach, W.A., 6020 Australia

Abstract.—In Bahía de la Ascensión, México, the fishery for *Panulirus argus* is based on artificial shelters called "casitas." Highest catch-per-unit-effort (kg tails/boat·day) in the fishery occurs each year immediately after the opening of the fishing season, and declines sharply over the next months. This trend probably reflects combined effects of natural mortality, fishing mortality, and emigration of lobsters from the bay.

In 1985, 3470 tagged lobsters were released during the closed season, and 849 (24.5%) were recaptured by fishermen, mainly during the first three months of the following fishing season. In 1986, an additional 1324 tagged lobsters were released, and 407 (30.7%) were subsequently recaptured. Growth of recaptured lobsters was highly variable, and sexes had different growth rates, that of males being higher. Von Bertalanffy parameters for each sex were calculated using two different techniques; most reasonable estimates were obtained by a maximum likelihood approach. Ninety-nine percent of the recaptured lobsters were caught within the bay, but movements generally tended to be toward the reef in front of the bay. Longest straight-line distance moved was 45 km.

The population fished in the bay was composed entirely of juveniles, and we hypothesize that an unfished population of adults exists outside the bay. Testing of this hypothesis would benefit future management plans. In addition, the long-term effects of casitas on the lobster population and on the ecology of the seagrasses and their associated benthic communities need to be understood.

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Panulirus argus accounts for approximately one-third of México's spiny lobster production of about 2400 t (mean for 1978–87), 80% of which is produced in the state of Quintana Roo (Secretaría de Pesca 1987). The fishery for lobsters in Bahía de la Ascensión began in 1965. Initially, traps and skin diving were used, but in 1968 "casitas cubanas" were introduced (Miller 1982). These "casitas" consist of a frame of about 1.8 × 1.2 m made of the trunks of a local palm, and a "roof" of the same wood, metal, asbestos or, more recently, ferrocement. Casitas are sunk over seagrass-covered bottom. The fishermen check the casitas by skin diving, and catch the lobsters with a gaff (Lozano et al. 1989). The bottom of the bay suitable for setting casitas has been divided into several parcels of different sizes, alloted to the older fishermen. Miller (1982) suggested that the casitas might increase the fishing pressure on the population and cause overfishing, and Eggleston et al. (1990) propose that casitas provide critical refuge for juvenile lobsters from their predators. The long-term effects of casitas on the lobster population remain to be determined.

Here we report the results of an investigation using tag and recapture methods to study the structure, movements, and growth rates of the spiny lobster population in Bahía de la Ascensión during 1985–87.

Methods

Fishing methods in Quintana Roo

The coast of Quintana Roo can be divided into three areas on the basis of the lobster fisheries (Fig. 1a):

In the northern area, from Holbox to Tulum and especially around Isla Mujeres, the fishery is well developed. Lobsters are caught mainly by traps in depths of 15–60 m, and by Scuba and "hookah" diving to depths near 40 m. An annual migration of lobsters occurs along the northeastern coast of the Yucatan Peninsula in a southerly direction, at the end of autumn or in winter (Kanciruk and Herrnkind 1978). During this migration, fishermen use lobster bottom-nets in areas 2–10 m deep. Twelve cooperatives, involving 65% of the 1084 lobster fishermen of the state, operate in the northern area.

In the central area, where Bahía de la Ascensión is located, skin diving and "casitas cubanas" are used. In this area, where three cooperatives

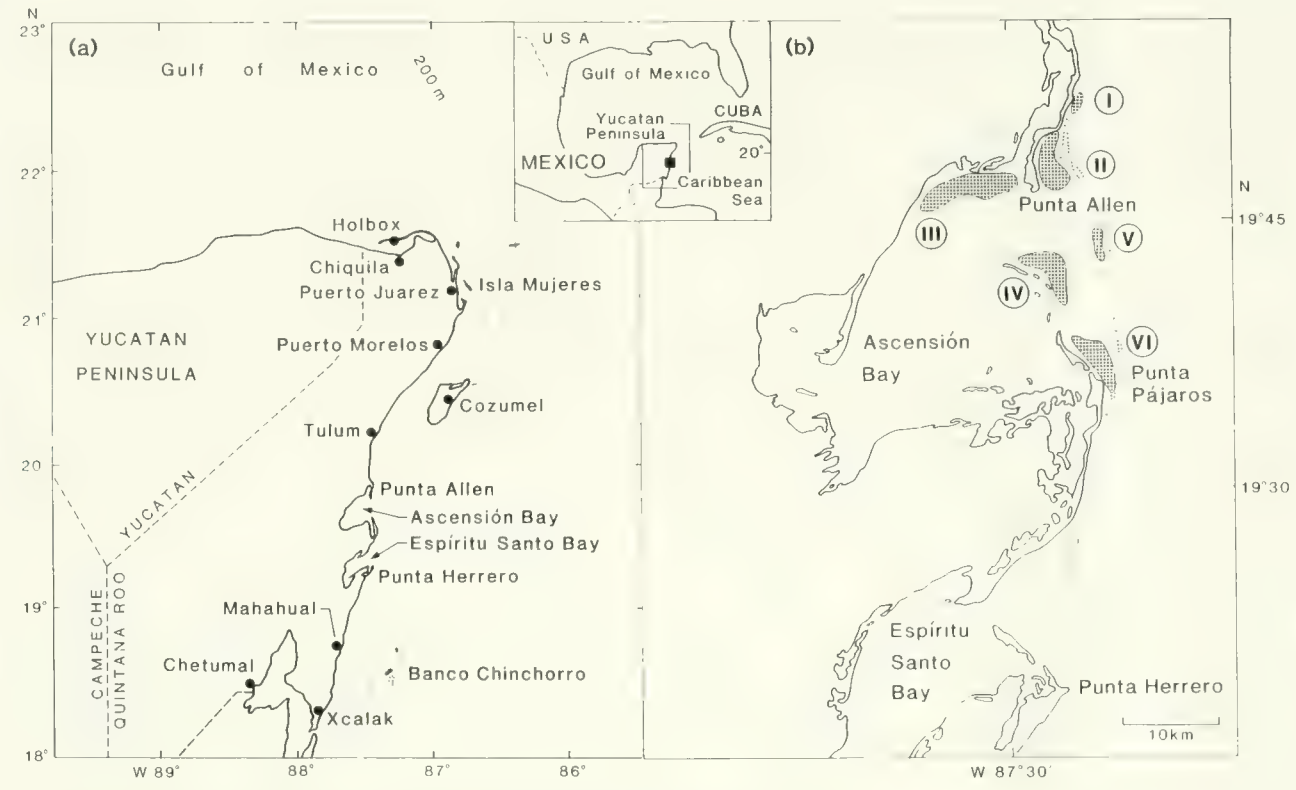

Figure 1

(a) The coast of Quintana Roo, showing the main fishing localities for *Panulirus argus*. (b) The six sampling zones for tagging operations in Bahía de la Ascensión.

with 21% of the fishermen operate, lobster fishing is limited to a depth of approximately 15 m.

In the southern zone, including Chinchorro Bank, three cooperatives involving 14% of the fishermen catch lobsters exclusively by skin diving with a gaff, to a depth of approximately 15 m (Secretaría de Pesca 1987).

Study site

Bahía de la Ascensión (Fig. 1b) is an open, shallow bay (<6 m) approximately 740 km^2 in area. Several coral banks follow an ancient shore line along the mouth of the bay (Jordán 1988) and form an interrupted reef. This reef reduces wave surge, and hence the bay has relatively calm waters.

The bay is bordered by mangrove and grass swamps and has several mangrove keys in its central and southern parts. The outer half of the bay is dominated by hard, sandy substrates with extended seagrass areas, whereas the inner half of the bay is shallow (<2 m), with mostly soft, unconsolidated sediments.

The fishery

Up to a maximum of 108 lobster fishermen in the area belong to a cooperative named "Pescadores de Vigía Chico," based at Punta Allen. A team that fishes the casitas in an owner's parcel during the fishing season consists of two or three fishermen (the parcel owner and one or two assistants). The number of casitas per parcel varies, and some owners claim to have more than 1000. The total number of casitas in the entire fishing ground of the cooperative was estimated at approximately 20,000, based on interviews of all fishermen in the cooperative. The fishermen catch lobsters mainly in the outer half of the bay, where seagrass is more abundant. There are no parcels in the inner half because the bottom is not suitable for casitas and the water is usually too turbid for diving. Regulations for this fishery include a closed season from 16 March to 15 July, a minimum size limit of 135 mm tail length (≈74 mm carapace length), and a prohibition on the catching of egg-bearing females. Only the tails are utilized. Tails are graded according to weight, packed in 10-pound (4.650 kg) boxes, and frozen.

Detailed data on monthly production (in boxes) of the cooperative during the 1985–86 fishing season were obtained from the processing plant. The relationship between tail weight (TW, in g) and carapace length (CL, in mm) was estimated by linear regression expressed as a power equation,

$$TW\ (g) = 0.00203\ CL\ (mm)^{2.5503}$$

where $N = 98$, $r^2 = 0.98$, CL range = 44.7–137.9 mm.

Data on catch in kg/tail weight of each fishing team were available since 1981 and converted to catch-per-unit-effort (CPUE, catch/boat·day). A Leslie analysis (Leslie and Davis 1939) was applied to the CPUE data to estimate the fishing mortality (F).

Tagging

Lobsters were tagged in Bahía de la Ascensión during 16 April–14 May 1985, and 18 May–30 June 1986, i.e., during the closed season. The area of the bay where casitas are distributed was divided into six sampling zones (Fig. 1b). Lobsters were tagged in all zones during 1985, and in zones II–VI in 1986. Chittleborough's (1974) western rock lobster tags were used. Only animals ≥ 44 mm CL were tagged in order to reduce incidental mortality which might occur on smaller animals (Chittleborough 1974). Tags were inserted into the dorsolateral extensor muscle between the cephalothorax and first abdominal segment. After tagging, the lobsters were immediately released where they had been caught. Underwater observations revealed that after a few minutes, the tagged lobsters returned under the same casita.

Tag number, date, release location, sex, reproductive state, and CL (± 0.1 mm measured from between the rostral horns to the posterior dorsal edge of the carapace) were recorded. Fishermen were requested to keep the head of a recaptured lobster with its tag so the CL could be measured, and to provide the recapture date and location. The tagging program was advertised widely, and a reward was offered in the form of a lottery to encourage tag returns.

Analyses of growth data

The analysis of growth using capture-recapture data was performed using Fabens' method (1965), and a technique developed by M. Palmer (CSIRO Div. Math. Stat., Floreat Park, W.A. 6014, Australia). This technique assumes an individual lobster grows exponentially with time:

$$y = a\,(1 - e^{bt}) + E$$

where y = CL (mm), a = asymptotic CL (mm), b = a growth coefficient, t = time, and E = residuals. A mean value of 6 mm CL obtained from 50 settling pueruli was introduced as a starting size (zero age) into the model.

Parameters for the model, including variability of individual growth, were estimated using a multivariate Gaussian distribution. The residuals around an individual's curve (E) were assumed to be independent Gaussian normal with constant variance. The likelihood estimate, assuming that individual coefficients are known for an individual, was

$$L_i = p\,(y \mid a,b)\ p\,(a,b)$$

where L_i = initial length, and p(.|.) denotes a probability distribution.

Since the individual animal's coefficients were unknown, we consider them as "nuisance" parameters and integrate them out of the likelihood, giving

$$l_i = \int_{-\infty}^{\infty} p\,(y \mid a,b)\ p(a,b)\ da\,db$$

where l_i is the likelihood for the i^{th} individual. Then the product of the individual likelihood must be maximized to find the estimates of the population parameters. A convenient algorithm to use in this case is the EM algorithm (Dempster et al. 1977). Details of its application in this context are in Laird et al. (1987), Palmer (1986), and Palmer et al. (1988).

Although the time between subsequent captures was known, the age at first capture was unknown. A probability distribution for this unknown parameter was also assumed, but now the initial time is treated as "missing" and is removed from the likelihood by integrating it out. The likelihood for the i^{th} animal is now of the form

$$l_i = \int_{0}^{\infty} \int_{-\infty}^{\infty} p(y \mid a,b,t_1)\ p(a,b)\ da\,db\,dt_1.$$

Maximum likelihood is used to estimate both the growth parameters and the distribution of initial ages. The method of constructing and maximizing the likelihood is described in Palmer et al. (1988).

Mean weekly growth rates (Hunt and Lyons 1986) of recaptured lobsters were analysed to determine if there were significant changes in growth rate along their size range.

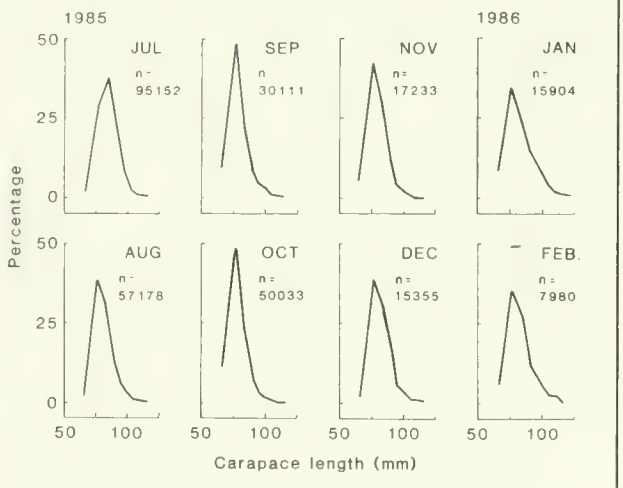

Figure 2
Monthly size-frequency distribution of the commercial catch (July 1985–February 1986) of *Panulirus argus* in Bahía de la Ascensión, obtained by converting tail weight (g) to carapace length (mm).

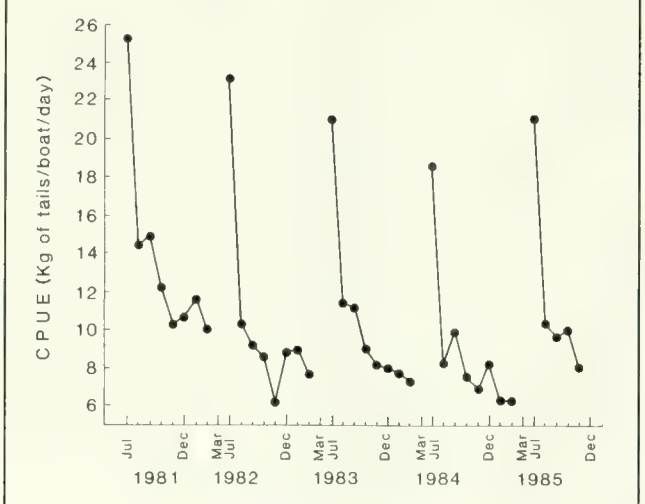

Figure 3
CPUE (kg tails/boat·day) of *Panulirus argus* for the fishing seasons 1981–82 to 1985–86 in Bahía de la Ascensión (no data available for January–March, 1986).

Results

Commercial catch and size composition

The total catch of lobster tails in Bahía de la Ascensión for 1985–86 was 42.5t, and for 1986–87, 63.0t. The size composition of the commercial catch for July 1985–February 1986 is shown in Figure 2. Data for March were insufficient and not included. There was a mode around the minimum legal size throughout the fishing season, except in July.

The CPUE (catch/boat·day) data trends were similar each year (Fig. 3). The highest CPUE occurred during 16 July–15 August, i.e., immediately after the opening of the fishing season, followed by a sharp decline over the next few months. This trend probably reflected both fishing and natural mortality, as well as emigration.

The values of F (fishing mortality), between 1.25 and 2.80, derived using a Leslie analysis (Leslie and Davis 1939) were highly influenced by the July data, which were the annual peaks (Fig. 3), implying a different F for that month. Therefore, the results of the analysis were biased and could not be considered a good estimate of mortality.

Tagging results

Of the total 3893 lobsters caught in 1985, 3470 were large enough to be tagged (Fig. 4a). The male:female ratio of the captured population was 1.14:1, and that of the tagged population was 1.13:1. Of the total 1403 lobsters caught during 1986, 1324 were tagged (Fig. 4b). The male:female ratios of both the captured and tagged populations were 1.04:1. The size range of both sexes was similar for both years.

A total of 849 tagged lobsters were recaptured during the 1985–86 fishing season (24.5% of total tagged in 1985). None of the animals tagged in 1985 were recaptured during the 1986 tagging period. However, four lobsters tagged in 1985 were recaptured during the 1986–87 fishing season. The male:female ratio of recaptured animals was 1.14:1. Lobsters were recaptured in all sampling zones in the bay, as well as at some localities outside of the bay.

A total of 407 lobsters were recaptured during the 1986-87 fishing season (30.7% of total tagged in 1986); the male:female ratio was 1.08:1. In this season, no lobsters were recaptured outside the cooperative's fishing grounds.

In both fishing seasons, nearly all the recoveries occurred during the first three months of the season (e.g., Fig. 5).

Population structure

The mean CL (61.4mm, range 10.2–142.4mm) of lobsters caught in the Bay during 1985 was significantly smaller (z test, Hoel 1976; $z = 10.4$, $P<0.05$) than that of lobsters caught during 1986 (65.2mm,

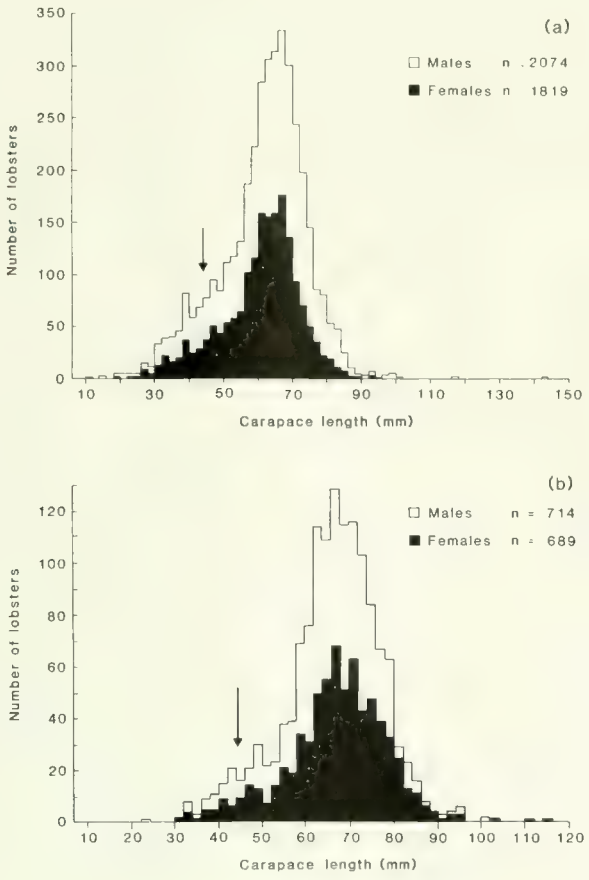

Figure 4

Size-frequency distribution of *Panulirus argus* caught in Bahía de la Ascensión for tagging purposes in (a) 1985 and (b) 1986. Tags were applied to lobsters ≥ 44 mm CL, as indicated by arrow.

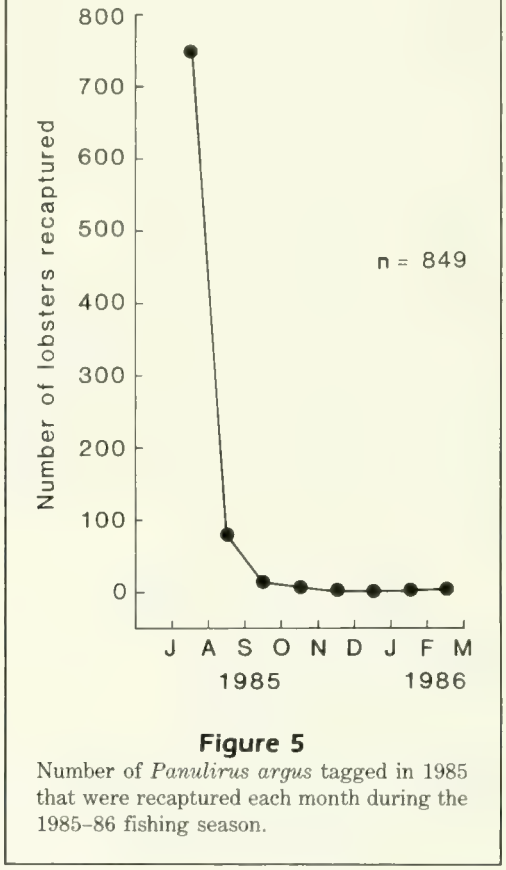

Figure 5

Number of *Panulirus argus* tagged in 1985 that were recaptured each month during the 1985–86 fishing season.

range 22.0 – 113.1 mm). However, the tagging operation in 1985 occurred one full month earlier than in 1986.

The means of CL of lobsters caught in each of the six sampling zones during 1985 and 1986 (Figs. 6, 7) were significantly different ($P<0.05$, approximate test of equality of means when the variances are heterogeneous; Sokal and Rohlf 1981, Box 13.2). An unplanned comparison among pairs of means (Sokal and Rohlf 1981) shows three groups of mean sizes in each year (Table 1). This result implies that the distribution of lobsters by size in the bay is not random. Smaller lobsters occupied the more interior of the six sampling zones (zones II, III, and IV), and larger lobsters occupied zones closer to the reef (zones I, V, and VI).

Growth and recruitment

Of the 849 lobsters recaptured during 1985–86 and the 407 recaptured during 1986–87, only 372 and 268, respectively, were returned with accurate CL information. All but two showed growth between tagging and recapture.

During the first three months of the 1985–86 season, the modal CL of recaptured males increased 10 mm. Growth of individuals was highly variable (Fig. 8) and in some cases indicates more than one molt occurred. For females (data not illustrated), the mode increased 8 mm.

Fabens' method (1965) for estimating growth parameters was used for both sexes and both years separately (Table 2a). The estimates of asymptotic length and the growth coefficient k by this method show great variability.

On the other hand, the EM algorithm needs some initial estimates before it can begin iterating, and the Fabens estimates were used for this. A set of data for males and females for each year was thus obtained (Table 2b). Combining the data over both years, for each sex, did not lead to a significant increase in the

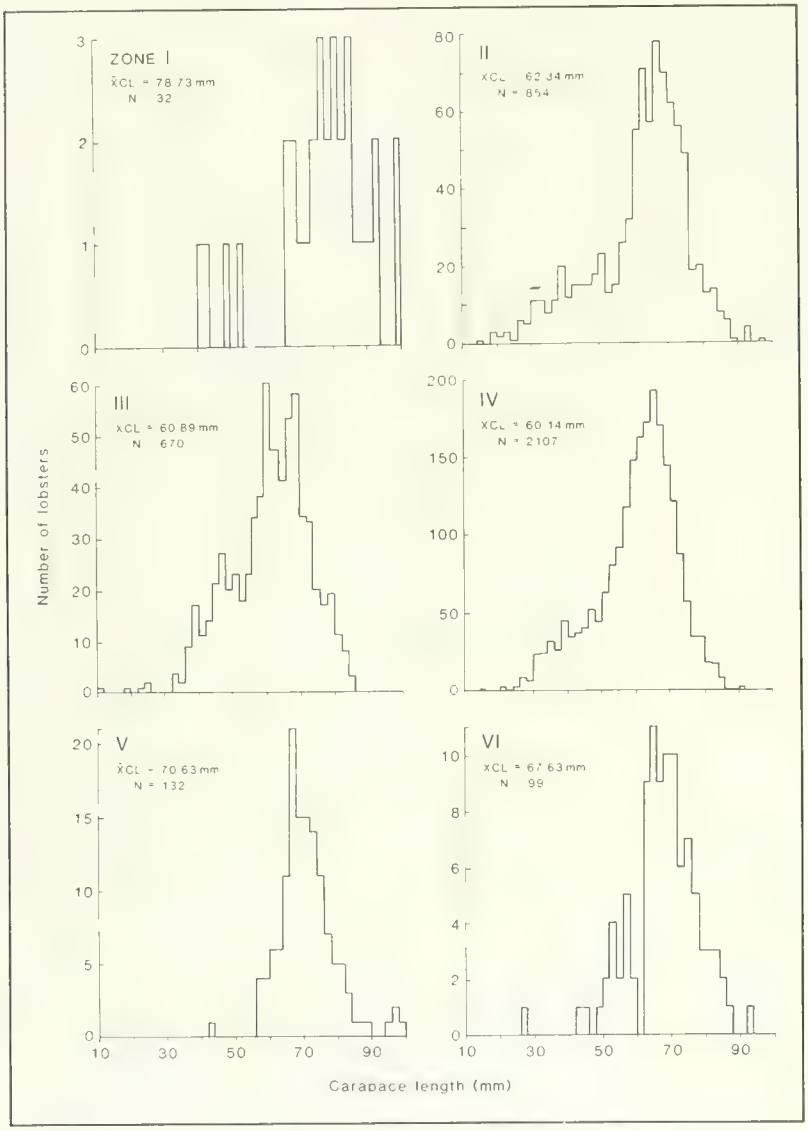

Figure 6
Size-frequency distribution of *Panulirus argus* caught in each sampling zone during the 1985 tagging operation in Bahía de la Ascensión.

log-likelihood ratio, indicating that it was valid to pool the data over the two years, i.e., there was no difference in growth between years. However, combining the male and female data led to a significant increase in the log-likelihood ratio, indicating different growth rates for males and females. Males grew faster and larger than females, similar to other panulirid species (Kanciruk 1980). The final set of data is shown in Table 2c. Estimated mean growth curves for males and females, combined for both years, are shown in Figure 9.

The algorithm also predicts the age at which each animal was initially caught. The estimated non-parametric density function of age at first capture for the 1985 and 1986 data showed a clear mode around 525 days from settlement.

Growth of the lobsters in Bahía de la Ascensión was rapid. Males and females enter the fishery at 74 mm CL, 1.65 and 1.7 years, respectively, after settling. Allowing for a six-month larval period (Lewis 1951), males and females enter the fishery at approximately 2.15 and 2.2 years of age, respectively.

The analysis of mean weekly growth rates (Hunt and Lyons 1986) combining the 1985 and 1986 data (not illustrated) did not show any points of inflection, suggesting that there is no marked decrease in the growth rate of the lobsters in the bay.

Movements

Most of the recaptured lobsters were caught within the boundaries of the cooperative's fishing ground. Lobsters that

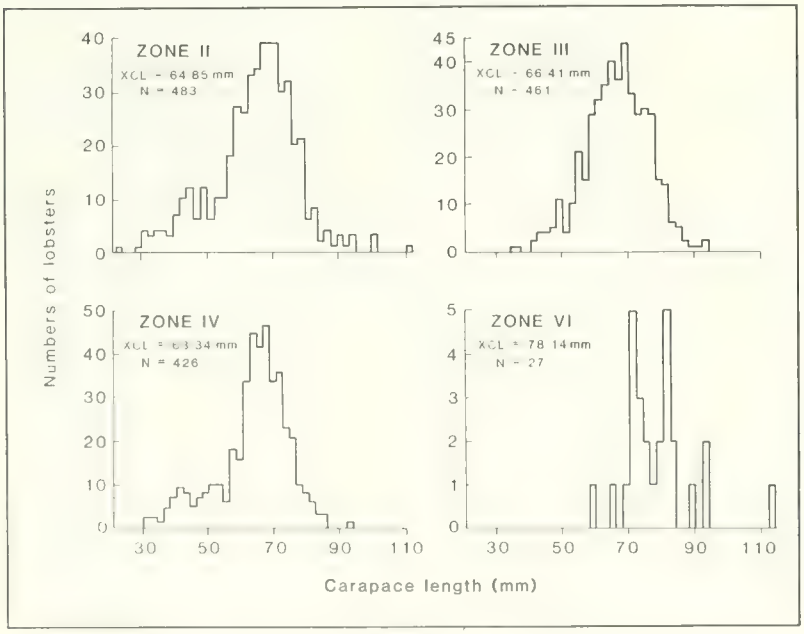

Figure 7
Size-frequency distribution of *Panulirus argus* caught in sampling zones II, III, IV, and VI during the 1986 tagging operation in Bahía de la Ascensión.

Table 1

Mean carapace length ($\bar{x}$ CL mm) of *Panulirus argus* caught in each of the six sampling zones. In 1986, no sampling was performed in zone I, and only five individuals were obtained in zone V. Mean CL's followed by corresponding letter in row are not significantly different ($P>0.05$). Means with different letter in row are significantly different ($P<0.05$), using test for unplanned comparisons among pairs of means.

	Zone					
	IV	III	II	VI	V	I
(a) 1985	60.14[a]	60.89[a]	62.34[a]	67.63[b]	70.63[b]	78.73[c]

	Zone			
	IV	II	III	VI
(b) 1986	63.34[a]	64.85[ab]	66.41[b]	78.14[c]

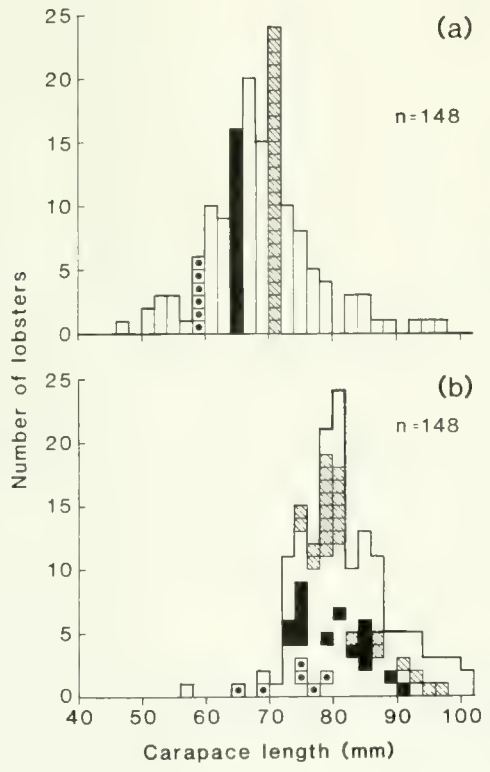

Figure 8

(a) Size at initial capture of 148 male *Panulirus argus* tagged at Bahía de la Ascensión, and (b) size of same males at recapture during first three months of 1985–86 fishing season. Shadings denote individual lobters and show carapace length increment by selected size cohorts, to emphasize variability in growth. It is possible that more than one molt is involved in some cases.

Table 2

Estimates of mean growth parameters for *Panulirus argus* form. $\hat{\Gamma}$ = dispersion matrix of the coefficients of the growth curve; $\hat{\sigma}^2$ = variability around an individual curve.

Ses	Year	L_∞	k
(a) Fabens' (1965) approach			
Males	1985	101.898	−0.0059
Males	1986	113.815	−0.0049
Females	1985	85.970	−0.0109
Females	1986	148.284	−0.0018
(b) Maximum likelihood approach (Palmer et al. 1988)			
Males	1985	255.464	−0.00057
Males	1985	261.501	−0.00054
Females	1985	222.807	−0.00065
Females	1986	218.149	−0.00067

$$\hat{\Gamma} = \begin{pmatrix} 10.295 & -0.00004 \\ & 2.16 \times 10^{-10} \end{pmatrix}$$

$$\hat{\sigma}^2 = 25.426$$

(c) Maximum likelihood approach (1985 and 1986 combined)			
Males		257.204	−0.00056
Females		215.605	−0.00068

$$\hat{\Gamma} = \begin{pmatrix} 10.349 & -0.000047 \\ & 2.19 \times 10^{-10} \end{pmatrix}$$

$$\hat{\sigma}^2 = 25.421$$

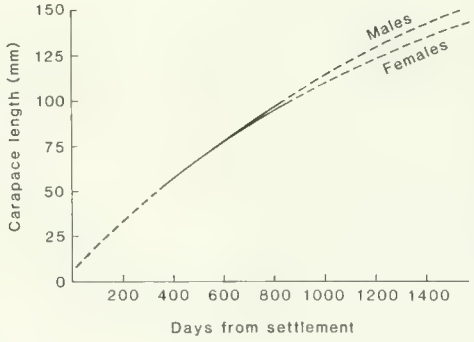

Figure 9

Growth curves for male and female *Panulirus argus*, as estimated by the maximum likelihood approach. Only the continuous lines are based on actual data; broken lines are extrapolations according to model.

dispersed from their zones of initial capture tended to move toward and along the reef in both years (Figs. 10, 11). As an example, of the 79 recaptured lobsters that had been tagged in zone III in 1985 (total number tagged in zone III = 581), 29 remained in zone III

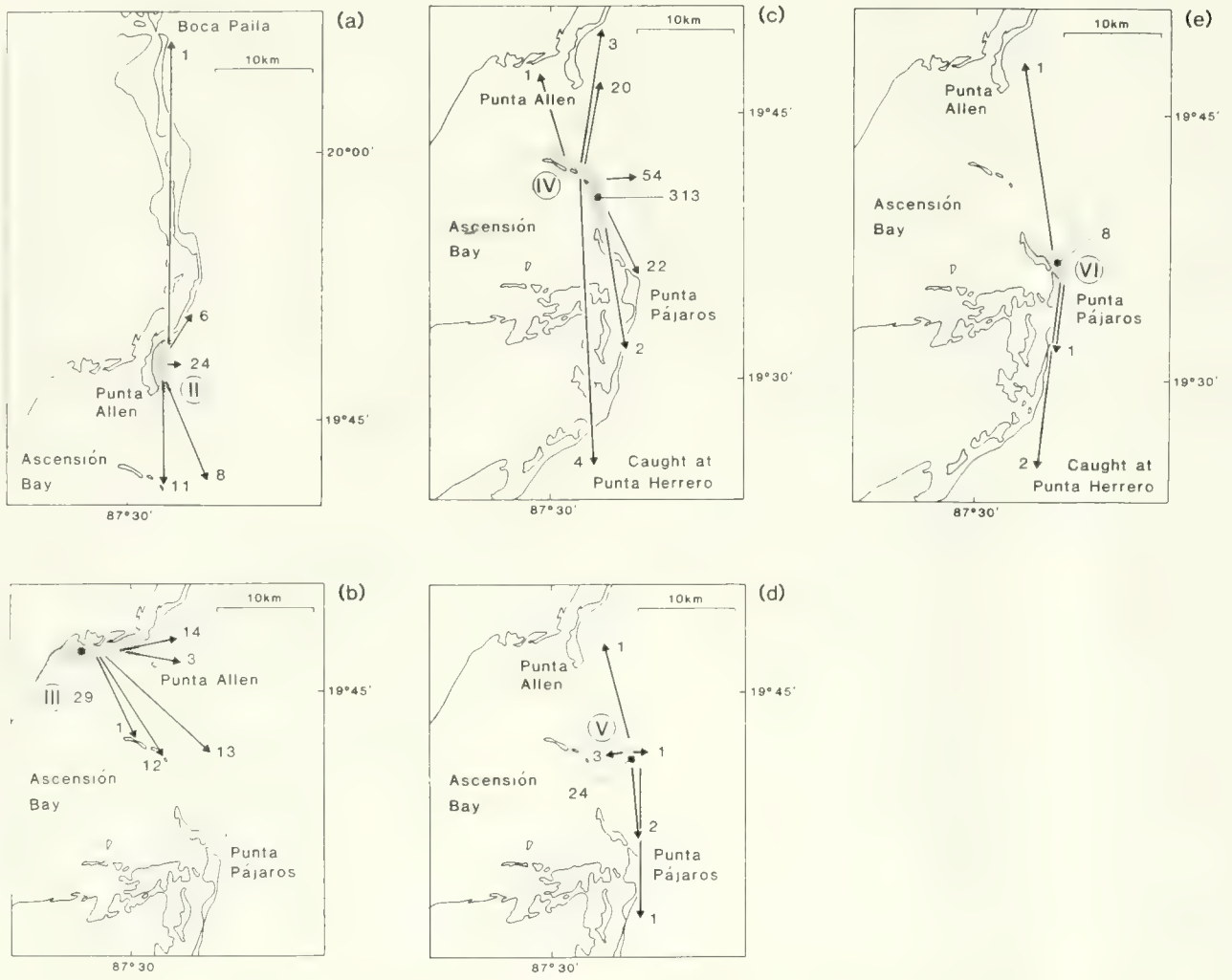

Figure 10

Recorded movements of *Panulirus argus* tagged in sampling zones II–VI in Bahía de la Ascensión, in 1985–86. Shaded areas denote sampling zones; arrows indicate direction of movements and arrowheads the sites of recapture. Numbers indicate lobsters that moved in each direction from denoted sampling zone.

and 42 moved to areas nearer or at the outer reef (Fig. 10b). However, because no lobster fishing was conducted in the inner half of the bay, no data have been obtained to indicate the possible movement of lobsters to that area.

In the 1985–86 fishing season, eleven lobsters were recaptured outside of the bay by fishermen of other cooperatives. Of these, ten had traveled south, while only one had gone north (Fig. 10). The longest straight-line distance traveled by an animal was 45km. All the recaptured lobsters that were tagged in 1986 were caught in the fishing grounds of the cooperative "Pescadores de Vigía Chico." The longest distance traveled by any of these was 23km (Fig. 11b).

No animals were caught north of Boca Paila or south of Punta Herrero (Fig. 10). However, fishing effort immediately outside the bay was restricted to skin diving on the reef to depths of about 15m, so any lobsters that moved beyond that depth would not be recaptured.

Reproduction

During the 1985 tagging program, only four individuals (67.2, 82.5, 83.7, and 116.8mm CL) of 1819 females had spermatophores attached, and only one individual (76.0mm CL) carried eggs. In the 1986 program, five individuals (87.0, 90.2, 94.2, 94.9, and 100.3mm CL)

of 689 females were found with remains of empty egg capsules and/or eroded spermatophores. In both years, all of the females that showed signs of reproductive activity were caught on the edge of the reef (zones II and V, Fig. 1b). No other evidence of reproductive activity was observed.

Discussion

A decline of CPUE from the beginning until the end of the fishing season has been reported for other *Panulirus argus* fisheries (Warner et al. 1977, Lyons et al. 1981). However, in the fishery of Bahía de la Ascensión, the decline from the first month of the season to the second is sharp. Eggleston et al. (1990) suggest that casitas enhance survivorship of juvenile lobsters by protecting them from their predators, hence increasing lobster production. Thus, during the closed season, in the absence of fishing mortality, it is possible that the aggregation effect of casitas on juvenile lobsters, in conjunction with recruitment by rapid growth, result in the catch from a casita being greater during the first month of the season than during the remainder of the season.

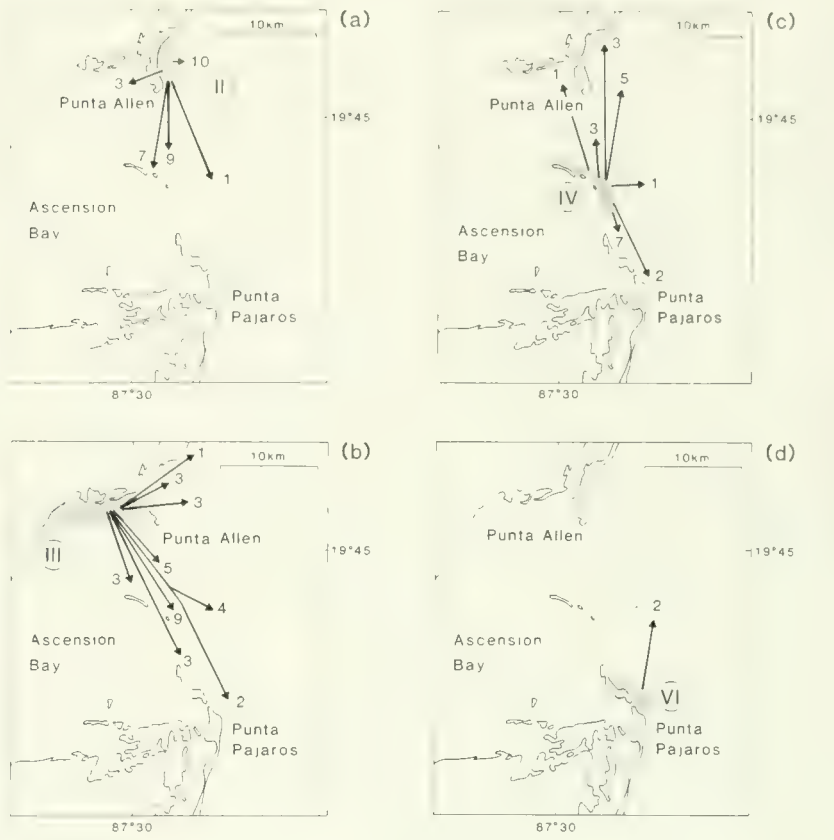

Figure 11

Recorded movements of *Panulirus argus* tagged in sampling zones II, III, IV, and VI in Bahía de la Ascensión, 1986–87. Shaded areas denote sampling zones; arrows indicate direction of movements and arrowheads the sites of recapture. Numbers indicate lobsters that moved in each direction from denoted sampling zone.

The high level of recaptures during both the 1985–86 and 1986–87 seasons suggests a high level of fishing mortality on the population in Bahía de la Ascensión. The failure to recapture any of the animals tagged in 1985 during the tagging program in 1986, and the fact that only four were recaptured during the fishing season in 1986–87, may reflect tag loss, high natural mortality, or a strong emigration from the bay. The latter is supported by the movements of the recaptured lobsters.

We could not separate fishing mortality from natural mortality because there appeared to be both recruitment by growth of small lobsters throughout the season as well as immigration onto the casitas from other areas. This is sustained by the monthly size composition of the catch by the fishery (Fig. 2). Those catches showed a nearly constant size distribution, with a mode near the minimum size limit, indicating recruitment by growth to the fishery throughout the fishing season.

The estimates of the growth parameters by the Fabens' method showed great variability (Table 2a), which could be interpreted in two ways: (1) Lobster growth differed greatly interanually, or (2) the procedure yielded unreliable estimates. Palmer et al. (1988) suggested that the Fabens method does not explicitly model individual variability in growth (e.g., Fig. 8), and that it produces inconsistent estimates of the asymptote of growth.

Alternatively, the maximum likelihood estimates of the mean curves did not show great variability, so both years could be pooled to obtain a final set of parameters. The reasonableness of the estimated parameters was further confirmed by the fact that *P. argus* can attain sizes much larger than the asymptotic sizes estimated from the Fabens method (Sutcliffe 1957, Munro 1974, Olsen and Koblic 1975, Farrugio 1975). However, the tagged lobsters were mostly juveniles and young adults as further demonstrated by the lack

of an inflection point in their mean weekly growth rate. Thus, the estimated parameters may reflect growth rates of immature lobsters only, and those of reproductive adults could change the last part of the curve (Fig. 9).

Lyons et al. (1981), utilizing a method that involved mean growth rates obtained from several authors, estimated an age of slightly more than two years after settlement as postlarvae for *P. argus* measuring 76mm CL, allowing for a nine-month larval period. With our maximum likelihood results, and considering the same nine-month larval period, the estimated age for a 76mm CL lobster would be 2.5 years. Munro (1974) produced a growth curve for *P. argus* based on data from 156 lobsters tagged and recaptured in Florida and Belize. His estimated age of one year after settling as postlarvae for lobsters measuring 45mm CL agrees closely with the estimate obtained in the present study by the maximum likelihood approach. Peacock (1974) tentatively estimated an age of one year for 50mm CL *P. argus*, as did Eldred et al. (1972) and Witham et al. (1968).

Therefore, the maximum likelihood approach utilized in this paper seems to have provided a useful set of growth parameters for juvenile and young adult *P. argus*, with the additional advantage of separating growth data between males and females.

The few signs of reproductive activity in female lobsters near the reef, in conjunction with small carapace length, indicated that the lobster population in Bahía de la Ascensión was probably composed mainly of juveniles. Lyons et al. (1981) found little evidence of mating activity of *P. argus* in the shallow Florida Keys, and they stressed that almost 90% of the spawning occurred at their reef and deep-water stations. Peacock (1974), Davis (1975), and Kanciruk and Herrnkind (1976) also reported an absence of reproductive activity in shallow bank or lagoon areas.

The movements demonstrated by the tagging program indicate a displacement of lobsters from shallows toward deeper habitats offshore. This was also supported by the analysis of the size composition by zones (Figs. 7, 8; Table 1), which indicated that the lobsters were smaller in the innermost sampling zones compared with those caught near or on the reef. Buesa (1970) and Cruz et al. (1986) suggested that juvenile *P. argus* in Cuba live in protected areas with seagrass beds and move towards the outer reefs as they grow. Other authors that mention similar movements for juvenile *P. argus* are Peacock (1974) in Barbuda, Olsen and Koblic (1975) in the U.S. Virgin Islands, Warner et al. (1977), Davis (1979), and Lyons et al. (1981) in Florida.

Although northern and southern movements were made by lobsters which left the bay, southerly movements predominated. In a three-year study of movements of *P. argus* in Biscayne Bay, Florida, Davis (1979) found southerly movements of tagged lobsters during the first year, northerly movements in the second year, and both northerly and southerly displacements during the third. He concluded that juvenile lobsters from Biscayne Bay are recruited into virtually the entire Florida fishery. The extent of the movements made through deeper water by the lobsters tagged in Bahía de la Ascensión—and their final destination—is still unknown, because from Tulum to Mahahual (Fig. 1a) lobsters are fished only in the bays and on the shallow parts of the reef. A winter migration, similar to that which occurs at the northeastern end of the Yucatán Península (Kanciruk and Herrnkind 1978), may take place in deeper waters outside the coral reef that runs across the front of the bay.

Small size, rapid growth, movements toward the reef areas, and lack of reproductive activity all serve as evidence that the population of lobsters in Bahía de la Ascensión is composed of juveniles. We hypothesize the existence of a population composed of reproductive adults off the coral banks of Bahía de la Ascensión, an area that is not currently being fished.

The existence of adult stocks outside of the bay and the output of lobsters from the bay into offshore deeper areas are issues that need to be assessed for future management plans. In addition, although casitas may provide critical refuge for juvenile lobsters from their natural predators (Eggleston et al. 1990), the long-term effects of the casitas on the lobster populations, as well as on the benthic communities associated with seagrasses and on the stability and structure of the seagrass beds themselves, remain to be determined through future field studies.

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Abstract.–Tilefish *Lopholatilus chamaeleonticeps* and yellowedge grouper *Epinephelus flavolimbatus* are deepwater fishes and targets of a relatively recent bottom longline fishery in the Gulf of Mexico. They are long-lived, slow growing, have very limited movements and distribution, and are susceptible to longlines. However, population size and life-history parameter estimates are generally unknown for Gulf fish. This study compared two methods for estimating population sizes to determine the most cost-effective one for use on long-term fishery-independent stock assessments. Bottom longlines were used to deplete fish from a small area, and a regression of catch per effort on cumulative catch was used to estimate the area's population prior to fishing. The population was also estimated by counting fish burrows from a submersible and expanding the mean number per unit area by the study site's area after correcting for the number of occupied burrows. Longlines and submersibles provided significantly different estimates of tilefish populations, the only species for which estimates could be compared. Longline estimates were probably more accurate because errors in area estimation and double counting were evident in submersible data. Longlines were less expensive to operate ($5000 vs. $8000 per day) and they afforded collection of size, age, and sex data on each fish caught. These data were not available from the submersible. Longlines could be used more cost-effectively than submersibles in determining long-term population changes. However, direct observation of fish behavior was not available from longlines, but was from the submersible. Submersibles also provide data on habitat and gear assessment, including deployment, efficiency, bait predation, and potential catch loss during retrieval.

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Comparison of Two Techniques for Estimating Tilefish, Yellowedge Grouper, and Other Deepwater Fish Populations

Gary C. Matlock
Fisheries Division, Texas Parks and Wildlife Department
4200 Smith School Road, Austin, Texas 78744

Walter R. Nelson
Southeast Fisheries Science Center, National Marine Fisheries Service, NOAA
75 Virginia Beach Drive, Miami, Florida 33149

Robert S. Jones
Marine Science Institute, University of Texas at Austin
P.O. Box 1267, Port Aransas, Texas 78373

Albert W. Green
Environment Assessment, Texas Parks and Wildlife Department
4200 Smith School Road, Austin, Texas 78744

Terry J. Cody
Coastal Fisheries Branch, Texas Parks and Wildlife Department
100 Navigational Circle, Rockport, Texas 78382

Elmer Gutherz
Mississippi Laboratory, National Marine Fisheries Service, NOAA
P.O. Drawer 1207, Pascagoula, Mississippi 39567

Jeff Doerzbacher
11505 Oak Branch Drive, Austin, Texas 78737

Tilefish *Lopholatilus chamaeleonticeps* support an economically important bottom longline fishery in the Mid-Atlantic Bight (Grimes et al. 1980, Turner 1986), and are the focus of a developing longline fishery in the South Atlantic Bight and the Gulf of Mexico (Katz et al. 1983, Low et al. 1983). Impacts of this development in the Gulf are unknown because population sizes and life-history parameter estimates there are generally unknown. However, the potential for recruitment overfishing appears large even at relatively low fishing effort because of the fish's life history (Harris and Grossman 1985). The fish is long-lived, slow growing (Turner et al. 1983, Harris and Grossman 1985), has limited movement (Grimes et al. 1983, 1986), and is restricted to temperatures of 9–14°C (Grimes et al. 1986, Freeman and Turner 1977). Tilefish are burrowers, requiring a clay substrate that is soft enough to allow burrowing, but firm enough for maintenance of burrows that may exceed 1 m in diameter and 3 m in depth (Able et al. 1982, Grimes et al. 1986, Twichell et al. 1985). In the Gulf of Mexico this is a narrow geographic area along the outer edge of the continental shelf between depths of 229 and 411 m (Nelson and Carpenter

1968, Wolf and Rathjen 1974). For the above reasons, tilefish are susceptible to capture on longlines (Nelson and Carpenter 1968, Wolf and Rathjen 1974, Grimes et al. 1982, Cody et al. 1981) and overfishing (Harris and Grossman 1985).

Yellowedge grouper *Epinephelus flavolimbatus* are also a target of the developing Gulf longline commercial fishery (Prytherch 1983, Graham 1978). However, even less is known about the life history and populations of this species than of tilefish. They are apparently present in commercial concentrations off Texas in the 128–274 m depth zone (Nelson and Carpenter 1968). On only 90 trips in the Gulf in 1982 over 65,000 kg of yellowedge grouper were landed (Prytherch 1983). However, their frequent distribution around rock and coral formations may preclude sustained commercial catches because of gear loss (Graham 1978).

This study was conducted to contrast "fishing out" an area with bottom longlines to direct visual observations from a small research submersible as methods for determining population sizes of tilefish, yellowedge grouper, and other deepwater fishes. The impact of longline fishing on these populations within a limited area was also determined.

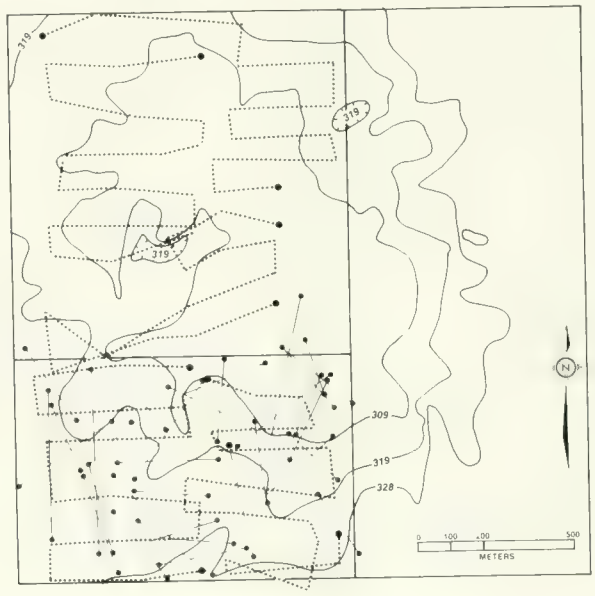

Figure 1

Tilefish study area (center point at 27°40.0′N lat. and 94°22.8′W long.) showing depth contours in meters, submersible transect tracks (dashed lines), and distribution of longline sets (solid lines) within the southern part of the study area. Chart represents one square nautical mile.

Materials and methods

Preliminary activities

In May 1984 the NOAA ship *Oregon II* spent 6 days surveying an area measuring 95 km east-to-west (94° 10′ long. to 95°00′W long.) between 183- and 457-m depths directly south of Galveston, Texas. Bottom configuration and acoustic signatures of fish were noted with a color-enhanced fathometer. Eleven bottom longline sets were made during each day to locate areas of high tilefish and yellowedge grouper catch rates (≥0.3 fish/100 hook-hours). Based on these preliminary cruises, specific sites were chosen for the submersible and longline studies described in this paper. Three days (10–13 September 1984) were spent by the *Oregon II* making detailed charts of each study site prior to the arrival of the submersible. Bathymetric charts of each site were developed using a depth sounder and Loran "C" plotter. These charts represented an area 2.6 km^2 (1 nmi^2) and were contoured by 10-m depth intervals. The trackline interval used in mapping was about one track per 15 m. The charts were duplicated and copies were provided to the Harbor Branch Foundation's RV *Johnson* prior to the beginning of submersible and fishing activities. This allowed both vessels to track and plot the position of the submersible and location of longline sets precisely.

Study area

Tilefish A study area (1.9 × 1.1 km) was selected off the north Texas coast at 27°40.0′N lat. and 94°22.8′W long. (Fig. 1). The area was a broad ridge with a minimum depth of 304 m. Approximately 50% of the study area was less than 311 m in depth with the bottom dropping gradually away to 316–318 m at the northern part of the area, and 320–329 m in the southwestern part. The area was almost entirely covered with a soft sand-clay mixture, characteristic of tilefish habitat along the entire U. S. eastern coastline (Freeman and Turner 1977, Able et al. 1982, Twichell et al. 1985, Grimes et al. 1986). However, the substratum was less cohesive than in east coast tilefish grounds. A fin-stabilized metal rod, dropped from a height of 1.2 m by the submersible's manipulator arm, penetrated 80–100 cm in the gulf and 20–30 cm on east coast tilefish grounds (C.B. Grimes et al., NMFS Panama City Lab., unpubl. data for Mid-Atlantic Bight and South Atlantic off Florida).

Many of the burrows in the study area were dug at an oblique angle into the substratum or into a sloping face, instead of perpendicular as is characteristic of east coast tilefish on flat bottom (Able et al. 1982, Grimes et al. 1986). It was evident that the low cohesiveness

of the sediment probably caused the frequently observed cave-ins and sloughing of sediment around the mouths of burrows. Extensive secondary bioerosion by galatheid crabs and other burrowers (similar to the mechanism described by Able et al. 1982 and Grimes et al. 1986) further weakens the structure, contributing to cave-ins of the burrow roofs dug at an angle. Consequently, large areas of up to 6 × 9 m appeared to be plowed or cratered. It is not known if these broad areas were caused by one or several tilefish within each of the "plowed areas," or if one or more generations of tilefish were responsible.

Other tilefish burrows found in the study site were more like the typical "vertical" burrows known for these animals (Able et al. 1982, Grimes et al. 1986). Vertical burrows are apparently more stable than oblique ones, requiring less constant re- excavation. Some burrows that had become inactive were filled with sediment at the shaft entrance, but they showed evidence of recent bioerosion around their margins from secondary burrowers. There were also extensive areas that contained numerous depressions, apparently remains of old structures that were 1–2 m across and 0.6–1.5 m deep. Concentrations of 15–20 such depressions, 6–8 filled-in burrows, and 2–5 active burrows were common in the study area.

Yellowedge grouper A study area (1.28 × 1.28 km) slightly inshore of the tilefish site was selected at 27°41.3′N lat. and 94°23.6′W long. (Fig. 2). Depth ranged from 267 m along a central ridge to 311 m at the outer edge of the study area. The area was characterized by isolated boulders and scattered low rock ridges concentrated in depths of less than 283 m. The bottom was comprised of a sand-clay mixture interspersed with rubble and shell. Patches of avalanche anemones (*Bolocera* sp.) and sea pens (*Penatula* sp.) were frequently attached in the vicinity of rubble and "hard bottom." Bottom temperature fluctuated little at the study site (12.0–12.9°C). Fishing activities were confined to a 640 × 640 m (409,600 m^2) quadrant of the study area because time available was shortened by bad weather.

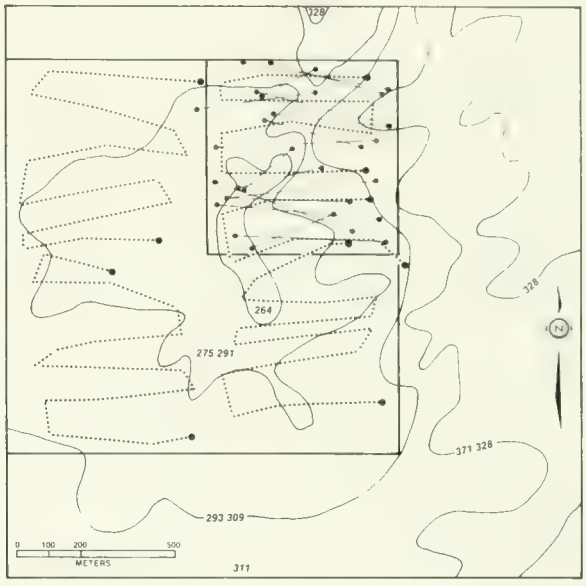

Figure 2
Yellowedge grouper study site (center point at 27°41.3′N lat. and 94°23.6′W long.) showing depth contours in meters, submersible transect tracks (dashed lines), and distribution of longline sets (solid lines) within the northeast part of the study area. Chart represents one square nautical mile.

Study activities

Submersible observations Burrow and fish counts were made from the submersible *Johnson-Sea-Link* during morning. Accordian-type transects with randomly selected starting points and alternating 366 (east–west) and 91-m (north–south) legs (up to 2652 m total distance per dive) were run with the submersible within 1 m of the bottom and traveling at 1.9 km/h. At the end of the east–west portions of each transect leg, the submersible would maintain position while the RV *Johnson* maneuvered directly above and recorded the position on a LORAN plot of the study area. Five transect dives were made on each of the study areas (Figs. 1, 2). Two of these transects were located completely within the portions of the tilefish area fished with longlines; one transect was completely within the fished portion of the grouper area.

The number of adult and juvenile burrows that were "filled-in" (denoting previous occupancy) or were "depressions" (characteristic of long-abandoned burrows that had been gradually filled in and smoothed over) were counted as inactive burrows. All others were counted as "active" (currently used by fish); only "active" burrow counts were used in estimating populations. Burrows within 7.3 m on either side of the submersible in the tilefish area and 11.0 m in the yellowedge grouper area were counted. These viewing distances were based on the range of visibility and viewing angles and were different in the two study areas because grouper and their burrows were generally larger than tilefish. So, grouper could be seen farther away than tilefish. All tilefish and yellowedge grouper seen were counted. All other fish seen were identified to species, if possible (names follow Robins et al. 1980), and these identifications were verified

using photographic and video records made during each dive.

Occupancy of "active" burrows was estimated by observing tilefish diving into burrows and by observing "smoking" (sediment plumes extruded) burrows during each of three other dives. These "positive" sightings provided a minimum estimate of occupancy of the total number of active-looking burrows seen on each dive. Occupancy dives were not conducted in the yellowedge grouper site, because grouper were usually seen outside their burrows and only moved out of sight into burrows when the submersible approached.

Bottom longline fishing Intensive fishing activities were conducted with bottom longlines in a portion of each study area (Figs. 1, 2). In the tilefish area longline sets consisted of 100 No. 7 circle hooks on 4.6-cm gangions, attached to a 366-m long ground line with halibut line snaps. Weights were used at both ends of the longline to prevent movement of the line along the bottom. Longlines were baited with squid and fished during daylight only. Two lines were fished on a rotating basis, with sets being soaked for approximately 2 hours. A maximum of eight sets (800 hooks) were made per day. In the yellowedge grouper area "Kali" poles were used to reduce gear loss caused by hanging on large boulders. This gear consisted of 40 2.4-m long PVC pipes weighted at one end and buoyed at the other, with 5 hooks 20.3cm apart on each pole separated vertically by about 0.5m. One pole was clipped to a floating mainline every 9m with a halibut line snap. The "Kali" lines had only the lower end of the PVC pipe and anchors touching bottom. The lines were set at randomly selected locations for approximately 2 hours, using squid for bait.

Upon retrieval of all longlines, number of hooks returned, number of baits returned, and catch by species were recorded. Catch-per-unit-effort (CPUE) was calculated for each set using number of hooks returned.

Data analysis

Population densities and sizes were estimated using the Leslie method modified by Braaten (Ricker 1975, p. 151) from longline catches of Cuban dogfish *Squalus cubensis*, gulf hake *Urophycis cirrata*, southern hake *U. floridana*, and tilefish in the longline-fished portion of the tilefish area; and barrelfish *Hyperoglyphe perciformis*, longspine scorpionfish *Pontinus longispinis*, southern hake, and yellowedge grouper in the longline-fished portion of the grouper area. A regression of CPUE (in number of fish/100 hook-hours) for each longline on adjusted (50% of each day's total catch) cumulative daily catch was calculated using least squares regression weighted by the inverse of variance in daily CPUE (SAS 1982). The cumulative catch was adjusted to reduce bias that can result from using the cumulative catch at the start or end of each fishing period (Braaten 1969). The X-axis intercept was the population estimate ($\hat{N}$) for the area fished. Associated 95% confidence intervals were calculated following Sokal and Rohlf (1981, p. 498). Catchability coefficients (for species caught on longlines with significant regressions) were equal to the slopes of the regressions (Ricker 1975, p. 150). The assumptions of this technique include constant catchability, geographically closed (within the study area) population (i.e. no recruitment or emigration), no natural mortality, and constant fishing effort (Ricker 1975).

Data from the submersible were used to estimate tilefish and yellowedge grouper populations ($\hat{N}$) within the area fished with longlines (fished) and the remaining portion of the study area (unfished). There were two transects made in the fished portion, and three transects in the unfished portion of the tilefish study area. There was one transect made completely in the fished portion, and four transects in the unfished portion of the yellowedge grouper study area. These populations were estimated as the product of the mean number of burrows or fish per km^2, the percent burrow occupancy (for tilefish only), and the total km^2 in the study area. The mean number of burrows or fish per km^2 ($\pm$ 1 SE) was estimated for each transect and each area using the mean and variance equations for the delta-distribution (Pennington 1983, 1986) after transforming the density data along each leg of each transect to natural logarithm. Differences in mean densities were tested using the t-test (Sokal and Rohlf 1981). Occupancy was estimated as the mean percent ($\pm$ 1 SE) from three dives using the "smoking" burrow data discussed previously using the ratio estimator (Cochran 1977). The variance of the population estimates ($\hat{N}$) based on burrow counts was calculated as the variance of a product (burrows/km^2 $\times$ percent occupancy; Goodman 1960). Differences in the population estimates resulting from the longlines and submersibles were tested using the t-test (Cochran 1977, Sokal and Rohlf 1981) and variances associated with the population estimates.

Results

Fish data from longlines and submersibles provided significantly different estimates of tilefish populations. Population estimates for yellowedge grouper could not be made from the longline data because it did not yield a significant regression (Table 1). The number of tilefish (with 95% confidence intervals in parentheses) in the

Table 1

Population estimates and 95% confidence intervals (CI) for fishes caught on longlines and observed during submersible dives on the tilefish and grouper study areas off Galveston, Texas during September 1984. Longline estimates for fishes other than tilefish and yellowedge grouper were made only for species with significant relationships between catch-per-unit-effort and cumulative catch (Ricker 1975). Submersible estimates were based on expansions of mean burrows or fish per unit area seen on one and two transects in the grouper and tilefish study sites, respectively, to the total fished area (836,067 m^2).

	Longline						Submersible		
Species	No. of days	*Y*-intercept (± 1 SE)	Slope (± 1 SE)	R^2	*F*	*N* (95% CI)	No. of transects	*N* (95% CI) based on burrows	*N* (95% CI) based on fish seen
Tilefish site									
Tilefish	7	4.026 ± 0.835	−0.050 ± 0.012	0.382	18.574**	81 (39–128)	2	446(364–522)[a]	134(121–147)
Cuban dogfish	7	5.410 ± 1.190	−0.084 ± 0.020	0.371	17.677**	65 (24–108)			
Gulf hake	7	0.491 ± 0.330	−0.005 ± 0.010	0.007	0.209NS				
Southern hake	7	1.874 ± 0.501	−0.043 ± 0.013	0.260	10.554**	43(−27–121)			
Grouper site									
Yellowedge grouper	3	0.914 ± 0.383	−0.030 ± 0.020	0.140	2.277NS		1	150(105–195)	150(118–182)
Southern hake	3	3.445 ± 1.154	−0.052 ± 0.020	0.320	6.587*	66 (9–170)			
Longspine scorpionfish	3	0.995 ± 0.287	−0.013 ± 0.013	0.066	0.983NS				
Barrelfish	3	1.713 ± 0.705	−0.027 ± 0.017	0.157	2.605NS				

[a]Mean percent occupancy of burrows was 35.6 ± 16.8 (95% CI).

fished portion of the study area was 81 (39–128) based on longline catches; the estimate from submersible data was 134 (121–147) based on observed fish (Table 1). These estimates were significantly different from each other ($t = 4.939$, df = 29, $P<0.05$). The estimated number of tilefish based on burrow counts (446, 364–522) was four to five times higher than either of the fish-based estimates. The estimated number of yellowedge grouper in the fished portion of the grouper area was 150 (118–182) fish based on submersible grouper data and 150 (105–195) based on burrow data (Table 1). Again, no comparable estimate was made from longline data.

The estimated number of tilefish seen per unit area was significantly ($t = 3.621$, df = 51, $P<0.05$) greater (about 30%) in the fished area than in the unfished portion of the study area. There were also significantly ($t = 5.899$, df = 42, $P<0.05$) more yellowedge grouper (about 68%) seen in the fished area than in the unfished area (Table 2). This same pattern was apparent in the burrow data for tilefish ($t = 3.737$, df = 51, $P<0.05$) and yellowedge grouper ($t = 6.381$, df = 42, $P<0.05$). In the unfished portion of the grouper study area, the mean number of yellowedge grouper burrows seen per km^2 (70, 95% CI = 62–78) was less than 50% of the mean number of yellowedge grouper seen (170, 95% CI = 154–186) (Table 2). However, the number of burrows seen in the tilefish study area in both the fished and unfished portions exceeded the number of tilefish seen by about 10 to 20 times.

Estimates using submersible data could not be made for southern hake, gulf hake, Cuban dogfish, longspine scorpionfish, and barrelfish since they were generally not seen from the submersible. However, longlines caught 322 of these fishes during the 12,000–13,000 hook-hours of fishing on the tilefish and grouper study areas. Longline catch rates declined through time for southern hake in both study areas and Cuban dogfish caught in the tilefish study area, but no significant change in catch rates was detected for gulf hake in the tilefish study area or longspine scorpionfish or barrelfish in the grouper study area. Therefore, population estimates and 95% confidence intervals were only made for southern hake and Cuban dogfish; 43 (−27–121) and 65 (24–108) fish, respectively, in the tilefish study area and 66 (9–170) southern hake in the grouper study area (Table 1). More species were seen from the submersible than were caught on longlines (Table 3), but more population estimates could be made from longline data than from submersible data.

Table 2

Mean number of tilefish and yellowedge grouper and burrows of each species seen per km^2 on transects by a submersible in areas fished with longlines (study sites) and adjacent areas. Mean number of tilefish burrows seen was multiplied by mean percent occupancy (0.36 ± 0.16) to estimate number of tilefish and grouper. Width of each transect was 14.6 and 22.0 m for tilefish and grouper areas, respectively. The number of transect legs (n) is indicated for each transect.

	Tilefish						Yellowedge grouper					
			Fish		Burrows				Fish		Burrows	
Area	Transect	n	$\bar{x}$	SE	$\bar{x}$	SE	Transect	n	$\bar{x}$	SE	$\bar{x}$	SE
Fished with longlines	A	11	109	24	1500	80	F	11	370	30	370	50
	B	13	150	29	1400	80						
	Pooled	24	134	13	1500	40						
Adjacent (unfished)	C	7	12	5	900	300	G	11	70	9	60	8
	D	11	109	19	900	40	H	11	300	30	120	20
	E	11	150	19	3400	70	I	11	100	20	50	9
	Pooled	29	100	7	1700	60	Pooled	33	170	8	70	4
Pooled		53	117	3	1600	30		44	220	7	140	6

Table 3

List of species caught on longlines and seen from submersible in the tilefish and grouper study areas. An X indicates presence; blank indicates absence.

Common name	Scientific name	Longline	Submersible
Tilefish	*Lopholatilus chamaeleonticeps*	x	x
Yellowedge grouper	*Epinephelus flavolimbatus*	x	x
Southern hake	*Urophycis floridana*	x	x
Gulf hake	*Urophycis cirrata*	x	
Cuban dogfish	*Squalus cubensis*	x	x
Longspine scorpionfish	*Pontinus longspinus*	x	x
Barrelfish	*Hyperoglyphe perciformis*	x	x
Night shark	*Carcharhinus signatus*	x	
Chain dogfish	*Scyliorhinus retifer*	x	x
Chub mackerel	*Scomber japonicus*	x	
Snowy grouper	*Epinephelus niveatus*	x	x
Beardfish	*Polymixia lowei*	x	x
Moray	*Gymnothorax kolpos*	x	x
Conger eel	*Conger oceanicus*		x
Argentines	*Argentine* sp.		x
Shortnose greeneye	*Chlorophthalmus agassizi*		x
Reticulate goosefish	*Lophiodes reticulatus*		x
Red hake	*Urophycis chuss*		x
Buckler dory	*Zenopsis conchifera*		x
Slimehead	*Gephroberyx darwini*		x
Deepbody boarfish	*Antigonia capros*		x
Longspine snipefish	*Macrorhamphosus scolopax*		x
Longtail bass	*Hemanthias leptus*		x
Yellowfin bass	*Anthias nicholsi*		x
Bladefin bass	*Jeboehlkia gladifer*		x
	Polylepion n sp.		x
Flatheads	*Bembrops* sp.		x
Scorpionfish	*Scorpanenodes* sp.		x

Discussion

Longlines appear to be a more cost-effective means of monitoring fish population changes than submersibles. However, longlines kill all the collected fish whereas submersibles do not. More data can be collected on each caught fish at a lower cost with longlines than with a submersible. Size, age, and sex data could be collected from longline catches at a cost of about $5000 per day (in 1984 U.S. dollars), while none of these data were available from the submersible even though it cost about $8000 per day to operate. Additionally, the tilefish population based on burrow data from the submersible may have been overestimated because (1) "active" burrows were overestimated, (2) width of each burrow-count transect was underestimated, and (3) double counting occurred when transects crossed or came close to crossing. The number of tilefish estimated from tilefish seen was about 50% larger than the estimate based on longlines, and was about four times less than the estimate based on burrow counts. The number of burrows may be more a reflection of population size prior to exploitation if this area was heavily fished prior to our study.

Tilefish populations were probably underestimated using longline data. But the amount of bias is unknown. Capture probabilities were not constant, and this usually leads to underestimates (White et al. 1982). Recruit-

ment and emigration rates are unknown, but were probably low. If they occurred, recruitment must have been less than emigration because the populations were depleted in the study area. As recommended by Ricker (1975), our fishing effort was concentrated into "a rather short period of time" to minimize the effects of violating this assumption and that of no natural mortality.

The grouper population based on submersible fish data may have been overestimated because the estimated number of fish exceeded the estimated number of burrows and double counting of fish probably occurred. On one dive, the same fish (based on a scar on the lower jaw) was seen four different times.

Additional research is needed to determine the impacts of each of the above factors on fish population estimates based on counts made from submersibles. Future burrow counts should include all burrows, not just apparently active ones. Transect width should be accurately measured by counting burrows only within the range of a fixed physical extension from the submersible. Occupancy rates for tilefish and yellowedge grouper should be determined in randomly selected areas at night when they are most likely to be in their burrows.

Although no significant relationship between CPUE and cumulative catch was found for grouper, a more intensive effort should be made before discounting this technique. Additional longline collections over a longer period for yellowedge grouper are needed to determine if using the Leslie method is feasible.

Longlines can potentially impact stocks of tilefish. The population estimate of tilefish in the study area (39–128) and the catch made by the intensive fishing effort (79) indicate that from 62 to 100% of the fish were taken out of the area by an effort of approximately 6000 hook-hours, which is a 1.5–2 day effort by a commercial longliner (Prytherch 1983). Catch rates in the northern Gulf of Mexico in 1982 averaged 1–6 fish per 100 hook-hours (Prytherch 1983). Based on the estimated population size within the area, the initial catch rates indicate that the longline effectively catches all fish out of an area that is at least 12 m wide. Some fish are attracted from greater distances (Grimes et al. 1982), and some near the longline are not caught. But the number removed from the population is equal to the length of the longline × a width of 12 m × fish density.

Estimates of the total portion of the Gulf of Mexico inhabited by tilefish have not been developed, but the optimal areas are limited by depth, temperature, and bottom type (Grimes et al. 1980, 1986; Grossman et al. 1985). This, combined with slow growth rate, longevity, and low natural mortality (Turner et al. 1983, Harris and Grossman 1985), indicate that overfishing could easily take place if substantial effort is expended in tilefish habitat. This is especially true in light of the susceptibility to mass mortalities caused by sudden temperature reductions (Hachey 1955). Data from South Carolina tilefish habitat show a substantial decline in catch rate and mean size over a 4–5 year period with low to moderate effort (Low et al. 1983). Further, the number of tilefish burrows per km^2 in the Middle and South Atlantic Bights in the early 1980s was 241 and 125, respectively (Able et al. 1987). These estimates are much lower than the 1600 burrows per km^2 in the Gulf of Mexico estimated in this study.

More extensive longline studies of yellowedge grouper catches are required to assess the effect of longlines on these populations. The population estimate of yellowedge grouper in the yellowedge study site from fishing activities was not significant, but the best estimate (26 animals) from the non-significant regression may be realistic. The regression indicated that similar fractions of the yellowedge grouper population (40%) would be caught at similar levels of effort as compared with tilefish, and similar impacts from the longline fishery might be expected. However, the results may not be analagous because different gear were used in the two areas.

While the association with hard substrate and high relief was expected for yellowedge and other groupers, the burrowing habits were not expected. A detailed description of grouper habitat and burrow characteristics have been provided by Jones et al. (1989). The finding that this species also inhabits burrows was especially significant. If this were the only habitat, it would limit their distribution and increase their susceptibility to fishing once they are located. However, this species is also associated with rock and reef habitat typical of other grouper species. This diversity of habitat should enhance the survivability of the species overall, but it makes a part of the population more susceptible to longline fishing.

The uneven distribution of tilefish and yellowedge grouper between fished and unfished areas was also unexpected. Reasons for the differential distribution are not apparent. But the effects of depth, temperature, and bottom type on the fish were probably involved.

This study demonstrates the need for additional research to estimate population sizes and life-history parameters for deepwater Gulf fishes to quantify the amount of fishing they can support. Routine monitoring of these populations could be accomplished with longlines fished during August through October. Limited data on tilefish and yellowedge grouper have been collected with bottom longlines by the National Marine Fisheries Service since 1968 (Table 4). However, the data are insufficient to identify trends.

Table 4

Mean catch (no./100 hook-hours) ± 95% confidence interval of tilefish and yellowedge grouper on NMFS bottom longline sets each month, 1968–84, in the area bounded by 27°37′–27°50′ lat. and 93°32′–95°21′ long. Numbers in parentheses indicate numbers of sets. Blanks indicate no data collected.

Species	Year	Jan.	Feb.	May	Aug.	Sep.	Oct.	Nov.
Tilefish	1968	9.5 ± 12.2 (8)						
	1973			20.8 ± 6.9			6.8 ± 5.2 (14)	
	1975							2.1 ± 6.2 (3)
	1976				7.1 ± 4.1 (8)			
	1977		9.1 ± 9.3 (6)		10.0 ± 12.9 (4)			
	1983				6.1 ± 3.4 (7)			
	1984			6.9 ± 8.0 (9)		3.1 ± 1.3 (57)		
Yellowedge grouper	1968	5.5 ± 8.3 (11)						
	1973			18.4 (1)			0.7 ± 1.2 (8)	
	1975							0.0 (1)
	1976				2.5 ± 6.0 (3)			
	1977		0.0 ± 0.0 (3)					
	1981					0.0 ± 0.0 (2)		
	1983				3.7 ± 6.7 (8)			
	1984			1.2 ± 2.1 (6)		2.1 ± 1.3 (16)		

Natural and fishing mortality estimates, growth rates, population structure, distribution throughout all life stages, and weight landed should be determined and used in population simulation models to assist managers in protecting these resources from overfishing. A fishery-independent sampling program using longlines is recommended for monitoring the status of tilefish, hake, barrelfish, longspine scorpionfish, Cuban dogfish, and possibly yellowedge grouper populations. This is a more appropriate source of fish for mortality estimates than are commercial landings (Low et al. 1983, Winters and Wheeler 1985) and can yield reliable population size estimates if catchability coefficients are known.

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Reproduction, Age and Growth, and Movements of the Gulf Butterfish *Peprilus burti**

Michael D. Murphy

Florida Marine Research Institute, Florida Department of Natural Resources
100 Eighth Avenue SE, St. Petersburg, Florida 33701

Mark E. Chittenden Jr.

Department of Wildlife and Fisheries Sciences, Texas A&M University
College Station, Texas 77843
Present address: Virginia Institute of Marine Science, School of Marine Science
College of William and Mary, Gloucester Point, Virginia 23062

Abstract.–Collections were made for gulf butterfish *Peprilus burti* along a cross-shelf transect at depths of 5–100 m in the Gulf of Mexico off Texas from October 1977 to July 1980. Butterfish mature at 100–160 mm fork length as they approach age I. Spawning occurs primarily from September through May, but length frequencies indicate it concentrates, or is most successful, in distinct "Winter" (late January–mid-May) and "Fall" (early September–late October) periods that coincide with downcoast, alongshore currents (toward Mexico). Gonad data and persistence of small fish indicate spawning in winter, but at a low level. Spawning probably occurs offshore and upcoast toward the northcentral Gulf. Surface currents of the cyclonic shelf gyre probably transport eggs/larvae inshore and downcoast to recruit to the bottom in water 5–27 m deep, used as nurseries by butterfish when they are 2–5 months old. Butterfish disperse offshore as they mature and congregate in 36–100 m depths when they are 9–12 months old. They average 130–146 mm in fork length at age I in the northwestern Gulf, but 120–124 mm at age I and about 170 mm at age II in the northcentral Gulf. Estimates for the von Bertalanffy growth parameters L_∞, K, and t_0 were 164 mm, 1.99/year, and −0.20 years, respectively, for pooled northwestern Gulf Winter cohorts and 141 mm, 2.69/year, and −0.06 years, respectively, for pooled Fall cohorts. Somatic growth ceases as spawning approaches in the northwestern Gulf, but fish from the northcentral Gulf show large annual size increments. Butterfish reach about 200 mm in fork length, the largest ones occurring in the northcentral Gulf. Apparent maximum ages are 1–1.5 years in the northwestern Gulf, and 2–2.5 years in the northcentral Gulf. Differences in population attributes suggest complete mortality at age I in the northwestern Gulf or some unknown combination of an offshore and permanent contranatant spawning or postspawning emigration of adults to the northcentral Gulf. The genus *Peprilus* shows zoogeographic differences in population dynamics near Cape Hatteras, North Carolina.

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The gulf butterfish *Peprilus burti* ranges in the Gulf of Mexico (Gulf) from the Yucatan Peninsula to Tampa Bay, Florida (Horn 1970) and may occur along the U.S. southeast Atlantic coast, depending upon its systematic status and range extensions during cold spells (Caldwell 1961, Collette 1963, Horn 1970, Perschbacher et al. 1979). This abundant species is important in the industrial fishery and is commonly discarded by the shrimp fishery in the northern Gulf (Roithmayr 1965, Franks et al. 1972, Gutherz et al. 1975, Chittenden and McEachran 1976). Recent exploratory surveys have found large, commercially valuable concentrations of *P. burti* in the northern Gulf (Vecchione 1987). A preliminary biomass estimate for this area is 177,000 MT per 10,164 square miles (Gledhill unpubl.).

The life history and population dynamics of this species have not been described in detail, only as brief notes in numerous faunal studies including Gunter (1945), Hildebrand (1954), Miller (1965), Franks et al. (1972), Christmas and Waller (1973), Chittenden and McEachran (1976), and Allen et al. (1986). The paucity of information reflects difficulty in age determination. Allen et al. (1986) found that hard parts such as otoliths, scales, opercula, and vertebrae were not useful in age determination.

In this paper we use an extensive set of length frequencies to infer age of *P. burti* and to describe size and age at maturity, spawning seasonality and areas, recruitment, seasonal distribution and movements, growth, maximum size and age, and weight-length, girth-length, and total, fork, and standard length relationships. We also discuss hydrographic conditions associated with spawning areas and recruitment, and zoogeographic differences in population dynamics in *Peprilus* near Cape Hatteras, North Carolina.

Methods

Collections for *Peprilus burti* were made along a cross-shelf transect in the Gulf off Freeport, Texas (Fig. 1) from October 1977 through July 1980 aboard a chartered shrimp trawler using twin 10.4-m (34-ft) shrimp trawls with a tickler chain and 4.4-cm stretched mesh in the cod end. Initial stations were located at depths of 9, 13, 16, 18, 22, 27, 36, and 47 m. Sampling was expanded to include stations at 5 and 24 m after November 1978 and at 55, 64, 73, 82,

*Contribution No. 1625 of the Virginia Institute of Marine Science, College of William and Mary.

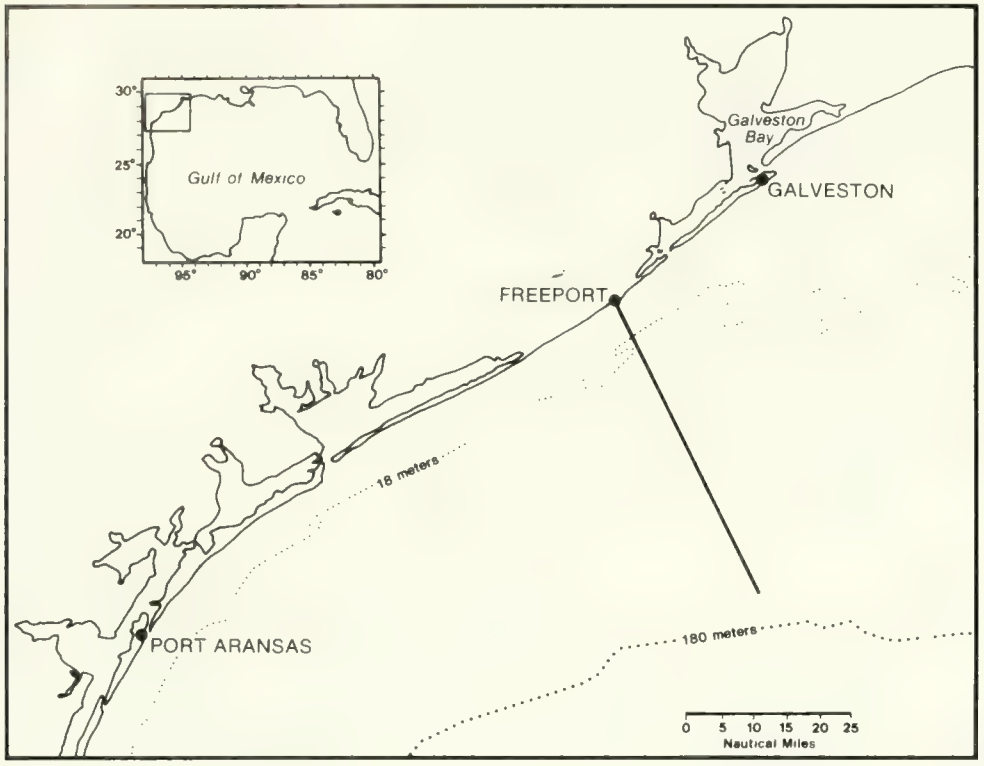


Figure 1
Location of sampling area off Freeport, Texas.

and 100 m after May 1979. Collections were made during the day through September 1978; thereafter, a day and a night cruise usually were made each month. Usually two tows, consisting of 10 minutes of bottom time, were made at each depth. Exceptions were 8 tows made at 16 m, and 24 tows made at 22 m, and only one tow made at most depths prior to October 1978. Our spatial sampling design was a single cross-shelf transect from a sampling frame that encompassed much of the northern Gulf.

All *P. burti* were culled from the catch, measured for total length (TL), fixed in 10% formalin for 2–4 days, and then stored in 70% ethanol. For the period December 1978–November 1979 a total of 300 fish, if available, was selected each month after stratifying the catch into cohorts determined by length-frequency analysis (see below). Specimens were then randomly selected within strata to determine total length, fork length (FL), standard length (SL), total weight (TW), gonad weight (GW), and girth (G) measured vertically from the dorsal fin to the preanal pterygiophore. Sagittal otoliths were removed from individuals larger than 75 mm, teased free of saccular and labyrinthian tissue, and then stored dry for later immersion in water and viewing with reflected light under a dissecting microscope. Female and immature fish were assigned gonad maturity stages (Table 1) modified from Kesteven's system (Bagenal and Braum 1971). Gonad weight and

Table 1
Description of gonad maturity stages assigned to immature and female *P. burti*.

Stage	Description
1 Immature	Gonads barely or not visible; sex indistinguishable to naked eye.
2 Maturing Virgin	Gonads small, opaque; usually thin, streamer-like, running along posterioventral wall of body cavity; sex indistinguishable to naked eye.
3 Early Developing/ Resting	Sex distinguishable; individual eggs not visible to naked eye but ovarian lamellae visible; ovaries occupy <20% of body cavity.
4 Late Developing I	Ovaries occupy 20–50% of body cavity; individual eggs visible in close examination; eggs opaque.
5 Late Developing II	Ovaries occupy 50–80% of body cavity; individual eggs distinguishable; eggs opaque.
6 Gravid	Ovaries occupy >50% of body cavity; translucent eggs present, but make up <50%.
7 Ripe	Ovaries occupy >50% of body cavity; >50% of eggs translucent.
8 Spawning/Spent	Ovaries flaccid, pink, with few eggs present; fish large enough to have spawned.

Table 2

Final quadratic growth regressions, calculated hatching dates, and von Bertalanffy equations for individual *Peprilus burti* cohorts and pooled Fall and Winter cohorts. Fits regress mean observed fork lengths (mm FL) on age in days (Days) for the quadratic and on age in years (Years) for the von Bertalanffy growth equations. All regressions are significant at $\alpha = 0.05$.

Cohort	Final quadratic growth equation	r^2	Final calculated hatching date	von Bertalanffy growth equation
$Fall_{77}$	$FL = 0.09 + 0.6004(Days) - 0.0007(Days)^2$	0.93	25 Sep 77	$FL = 139(1 - \exp(-2.22(Years + 0.050)))$
$Fall_{78}$	$FL = -0.14 + 0.6971(Days) - 0.0009(Days)^2$	0.87	8 Sep 78	$FL = 138(1 - \exp(-3.81(Years + 0.122)))$
$Fall_{79}$	$FL = -0.16 + 0.7234(Days) - 0.0010(Days)^2$	0.97	15 Sep 79	Data not adequate to fit alone
Fall pooled	$FL = 4.04 + 0.6386(Days) - 0.0008(Days)^2$	0.91	— — —	$FL = 141(1 - \exp(-2.69(Years + 0.063)))$
$Winter_{78}$	$FL = -0.10 + 0.1741(Days) - 0.0011(Days)^2$	0.95	30 Jan 78	$FL = 133(1 - \exp(-3.06(Years + 0.055)))$
$Winter_{79}$	$FL = 0.14 + 0.6931(Days) - 0.0008(Days)^2$	0.94	16 Mar 79	$FL = 170(1 - \exp(-1.98(Years + 0.043)))$
$Winter_{80}$	$FL = -0.09 + 0.6975(Days)$	0.93	22 Mar 80	Data not adequate to fit alone
Winter pooled	$FL = 8.18 + 0.6327(Days) - 0.0007(Days)^2$	0.93	— — —	$FL = 164(1 - \exp(-1.99(Years + 0.200)))$
Fall and Winter pooled	$FL = 6.28 + 0.6362(Days) - 0.0008(Days)^2$	0.91	— — —	

stage were also determined for randomly selected fish in October 1978 and during December 1979–February 1980 to verify spawning seasons. All lengths presented are fork lengths, and all length frequencies are moving averages of three, unless specified otherwise.

We also made collections in the northcentral Gulf, at depths of 9–91 m, aboard the FRS *Oregon II* east (89°00′W–89°30′W) and west (89°30′W–91°30′W) of the Mississippi River during 10–19 April 1980 and 21 April–1 May 1980, respectively (Rohr et al. 1980). Fish were sampled from these catches without randomization and measured (FL) to compare with size and age compositions in the northwestern Gulf.

Age was determined by length-frequency analysis, that is, the modal group progression analysis modification (Jearld 1983) of the Petersen method (Lagler 1956, Tesch 1971). Cohorts were specified by the season and year when they hatched, for example, $Fall_{79}$. Cohorts hatched during the periods January–May and September–October are hereafter referred to as Winter and Fall cohorts, respectively; this abbreviated terminology corresponds with the major spawning each period (see "Maturation and Spawning Periodicity"). Arithmetic means were used to describe central tendencies in cohort length frequencies.

Mean hatching dates used to approximate time scales to calculate growth were determined by a one-step iterative process following Standard and Chittenden (1984). A hatching date of 1 March was assigned to start iterations for the $Winter_{79}$ and $Winter_{80}$ cohorts because, in those groups, fish 30–75 mm, assumed to be 2–4 months old, first appeared mid-May to mid-June. A hatching date of 1 February was assigned to start iterations for the $Winter_{78}$ cohort because, in that group, fish 20–50 mm, assumed to be 1–3 months old, became abundant in mid-April. A hatching date of 1 September was assigned to start the approximation for Fall cohorts because fish 30–75 mm, assumed to be 2–4 months old, first appeared November through early December. Quadratic regression of length-on-age in days was then used to estimate initial x-intercepts for each cohort. Final hatching dates were calculated by using x-intercepts to readjust the initial x-variable (time) scale, so that each final quadratic growth curve passed through the origin (Table 2). Descriptions of spawning periodicity using length frequencies assume early size and age combinations (see Results) predicted from quadratic regression of length-on-age pooling all Winter and Fall cohorts (Table 2). Von Bertalanffy growth equations were fit to length and age (in years) data using the nonlinear least-square parameter estimation procedure in FSAS (Saila et al. 1988). Data points described a curvilinear regression and evidenced an asymptote, so equations presented met the minimum requirements for a von Bertalanffy fit (Knight 1968, Gallucci and Quinn 1979).

Maximum age was approximated by the Beverton–Holt model parameter t_L (Gulland 1969) following the definition that only 0.5–1.0% of the catch exceeds age t_L or its corresponding length (Alverson and Carney 1975, DeVries and Chittenden 1982). Maximum sizes and ages, and sizes-at-age, presented are termed apparent, because they may be affected by emigration of fish approaching age I; if so, they underestimate maximum size and age, and sizes-at-age.

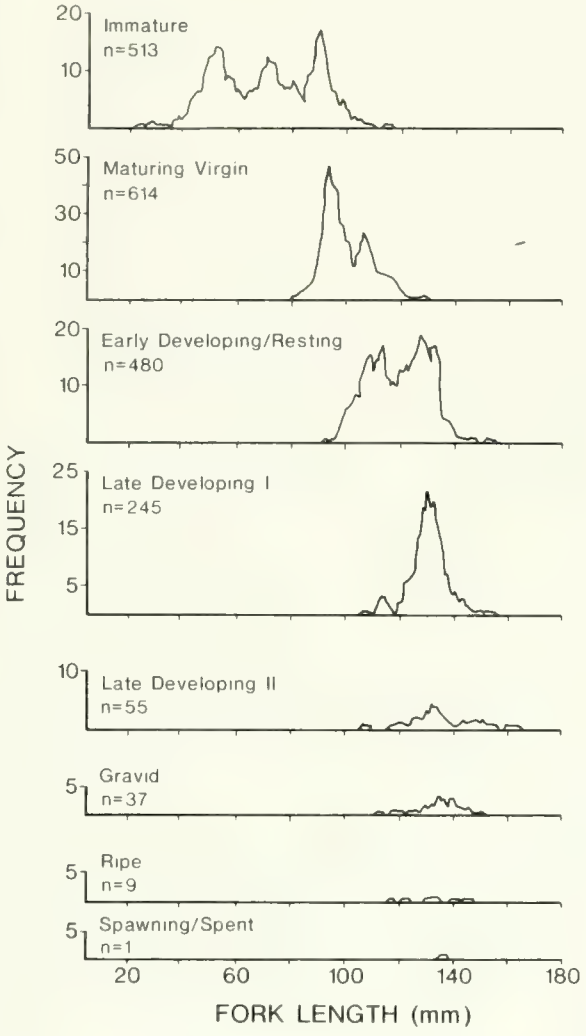


Figure 2
Length frequencies of immature and female *Peprilus burti* by maturity stage (see Table 1).

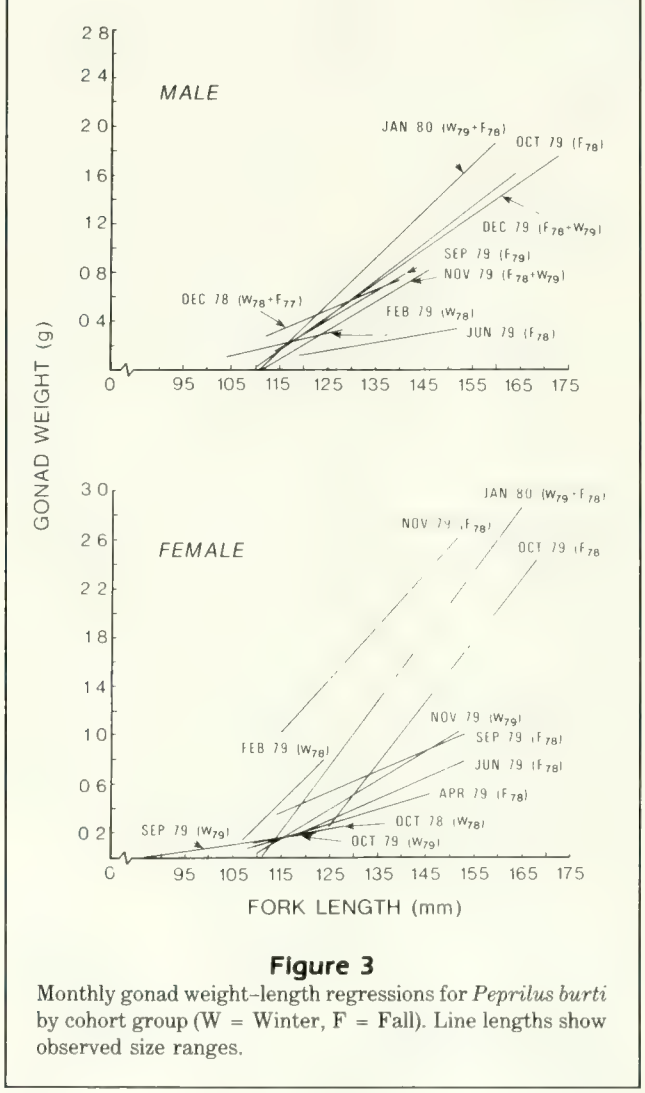


Figure 3
Monthly gonad weight–length regressions for *Peprilus burti* by cohort group (W = Winter, F = Fall). Line lengths show observed size ranges.

Figure 4
(facing page and overleaf)
Monthly length frequencies of *Peprilus burti* off Freeport, Texas.

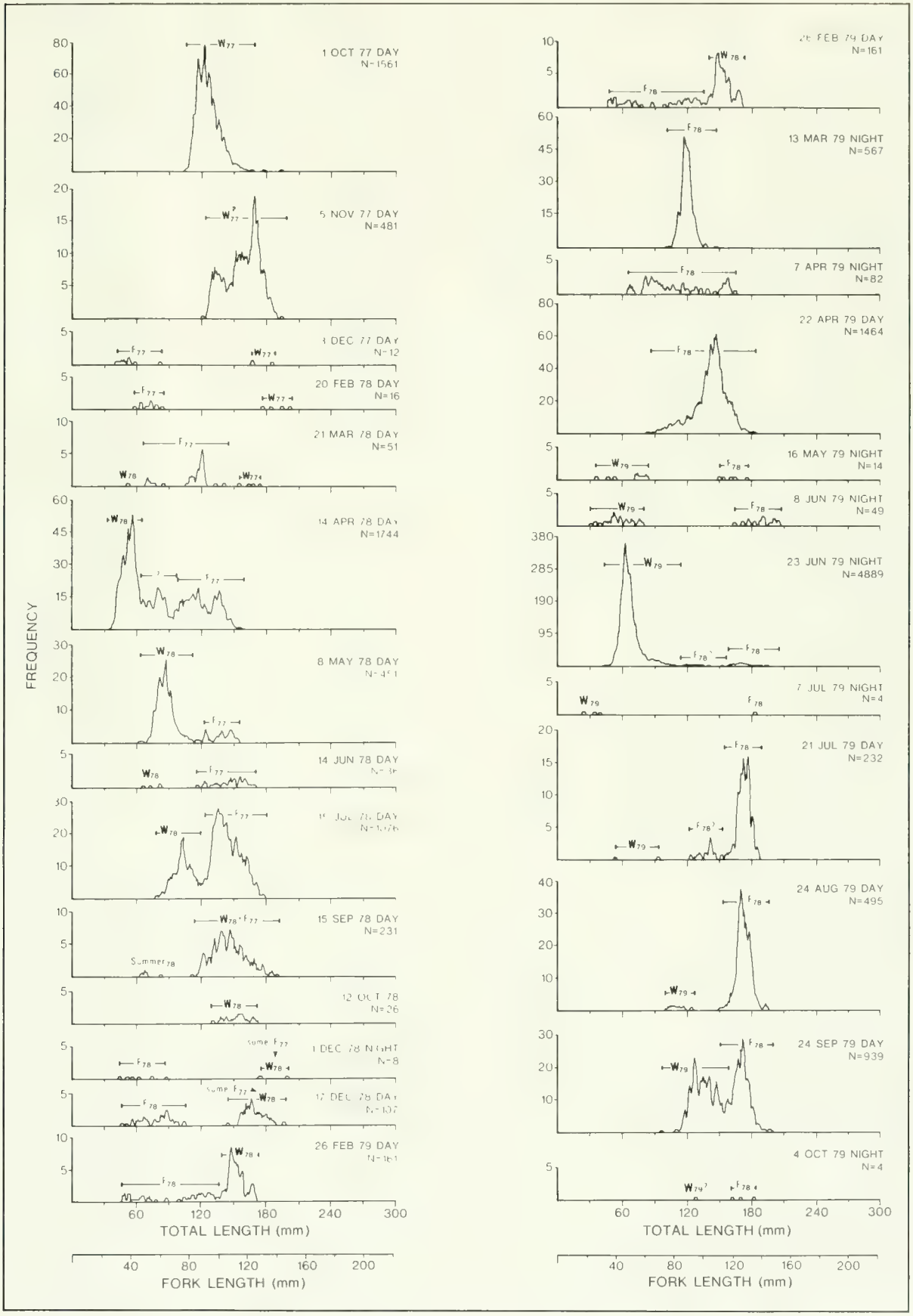
Results

Maturation and spawning periodicity

Peprilus burti mature at 100–160 mm in length. Few fish larger than 100 mm were immature (Fig. 2). Males were identifiable at 100–110 mm when the testes became creamy white, but they were difficult to stage macroscopically. Females were 95–155 mm and 105–165 mm in Early Developing and Late Developing stages, respectively. Most Gravid and Ripe females were 120–150 mm, the smallest being 113 mm. These sizes-at-maturity are supported by regressions of gonad weight on fork length (Fig. 3) in which x-intercepts for both sexes usually were 95–110 mm during September through February, a period that brackets much of the broad spawning period when fish should be maturing. Age compositions and sizes-at-age presented later indicate *P. burti* mature to first spawn at 9–16 months.

Peprilus burti spawn primarily during the broad period of September through May. Fish 30–40 mm, which occurred mid-November to early July (Fig. 4), were 1.5 months of age April–July and mid-November–December based on quadratic regressions of size-on-age for pooled Winter and Fall cohorts (Table 2).

Little spawning of *P. burti* occurs June through August. Fish 30–40 mm, 1.5 months-old, were not captured late July to early November (Fig. 4). No distinct,


1 OCT 77 DAY N=1561
5 NOV 77 DAY N=481
3 DEC 77 DAY N=12
20 FEB 78 DAY N=16
21 MAR 78 DAY N=51
14 APR 78 DAY N=1744
8 MAY 78 DAY
14 JUN 78 DAY
15 SEP 78 DAY N=231
12 OCT 78 N=26
1 DEC 78 NIGHT N=8
26 FEB 79 DAY N=161
13 MAR 79 NIGHT N=567
7 APR 79 NIGHT N=82
22 APR 79 DAY N=1464
16 MAY 79 NIGHT N=14
8 JUN 79 NIGHT N=49
23 JUN 79 NIGHT N=4889
7 JUL 79 NIGHT N=4
21 JUL 79 DAY N=232
24 AUG 79 DAY N=495
24 SEP 79 DAY N=939
4 OCT 79 NIGHT N=4
FREQUENCY
TOTAL LENGTH (mm)
FORK LENGTH (mm)

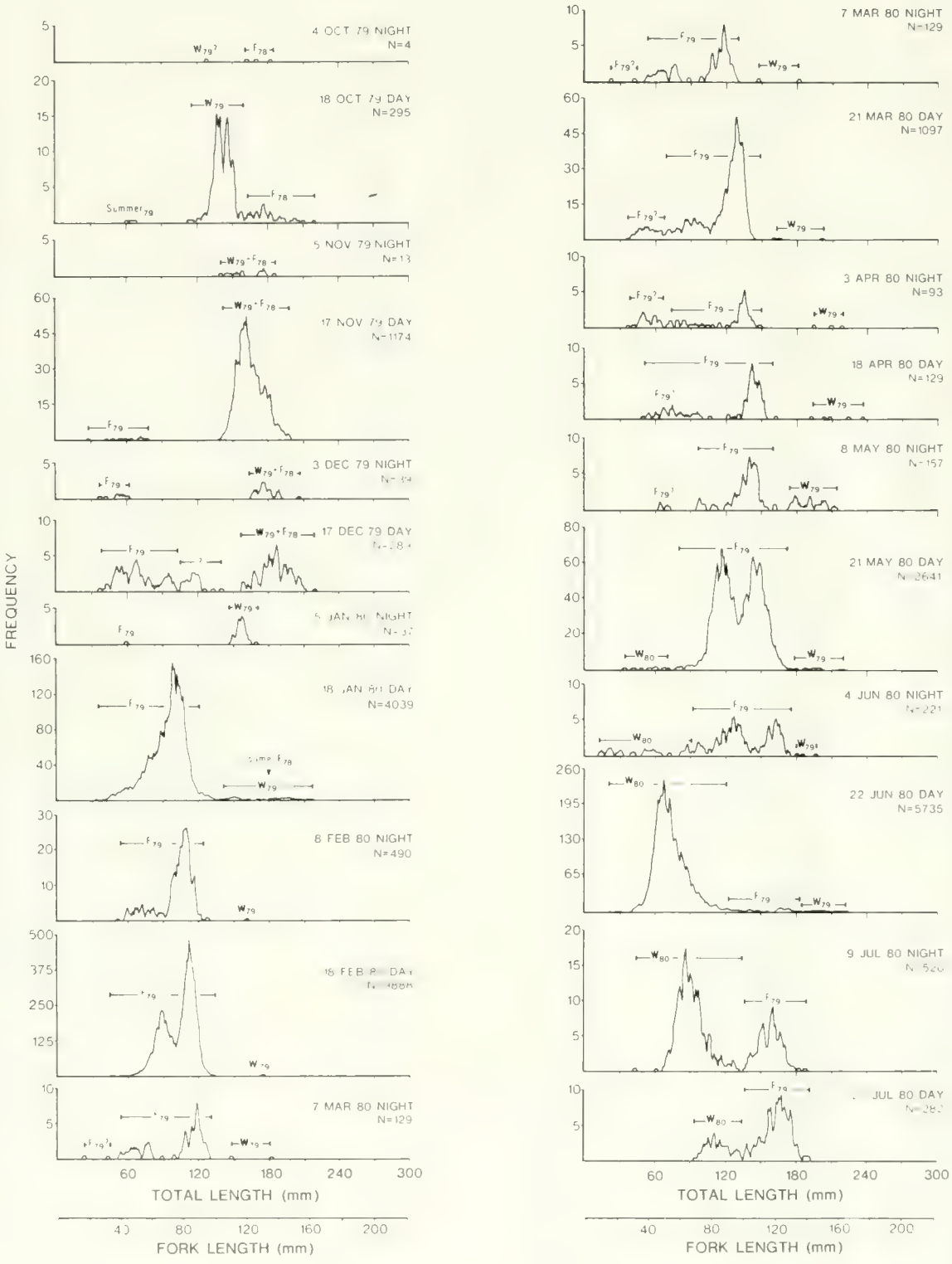


Figure 4 (continued)

abundant groups of fish 30–60 mm originated then, and the smallest fish caught then usually reflected the more slowly growing Winter-spawned individuals. The few fish 50–60 mm, about 2.5–3 months of age on average, caught September to mid-November, and the one Gravid fish captured in July, probably indicate some summer spawning (Fig. 5).

Peprilus burti spawn primarily during discrete Winter (late January–mid-May) and Fall (early September–late October) periods. Length compositions were consistently bimodal off Texas, and modal groups originated from Winter and Fall spawning periods (Fig. 4). Winter-spawned fish first appeared mid-April to early July at lengths of 30–75 mm at an average age of 1.5–4.5 months, which indicates spawning from about late January to mid-May. Fall-spawned fish first appeared mid-November to early December at lengths of 30–75 mm and an average age of 1.5–4.5 months, which indicates spawning from about early September to late October. Modes for Winter cohorts are readily followed in the periods: (1) mid-April 1978–late February 1979, (2) mid-May 1979–mid-June 1980, and (3) late May–late July 1980. Modes for Fall cohorts can be followed in the periods: (1) early December 1977–mid-July 1978, (2) December 1978–mid-October 1979, and (3) mid-November 1979–late July 1980. Calculated mean hatching dates occurred during late January to March for Winter groups and during September for Fall groups (Table 2).

In contrast to length frequencies, gonad weight and maturity data indicate *P. burti* spawns during much of the fall and winter. Gonad weight regressions had maximum slopes and elevations and usually were significant September through February (Fig. 3). Regressions had lower slopes and elevations and usually were not significant March through August (Murphy 1981, Table 2). Most Gravid and/or Ripe fish were captured November through February (Fig. 5).

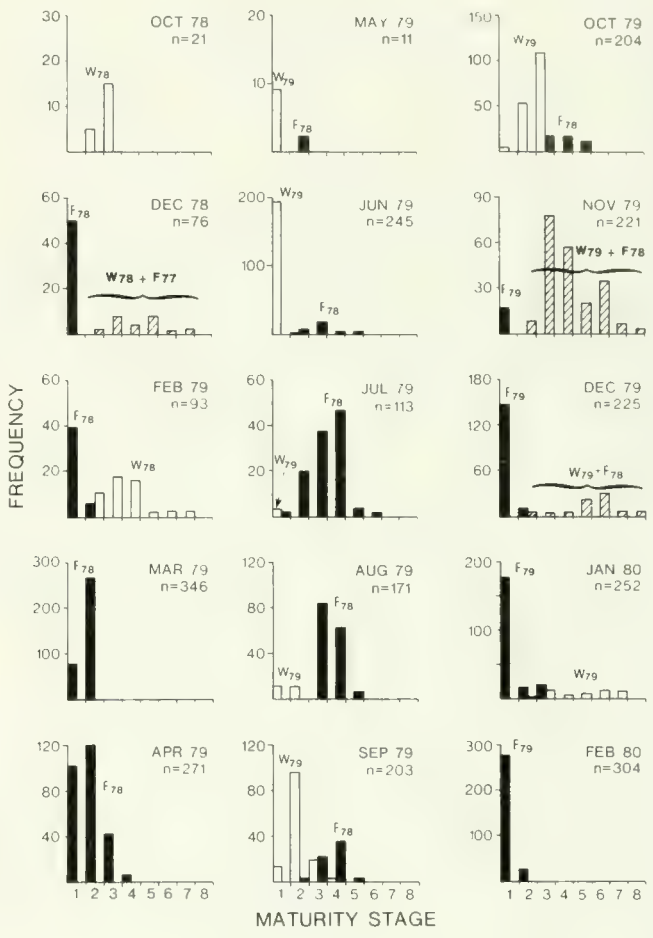


Figure 5

Monthly maturity stages (Table 1) of immature and female *Peprilus burti*. Bars indicate Fall (F, dark) and Winter (W, light) cohorts and mixtures of two cohorts (diagonals) in which cohort identity is not clear for individual fish.

The end of the Fall spawning period is not clear, but length frequencies suggest low-level spawning, or spawning success, during late fall and early winter. The consistently bimodal length frequencies must reflect some temporal separation in spawning that originates then. $Fall_{79}$ fish recruited in abundance by mid-January to mid-February 1980 when they were 60–105 mm long and 3–7 months of age (Fig. 4). $Fall_{78}$ fish recruited in abundance by mid-March 1979 when they were 90–110 mm and 5.5–7.5 months of age. These data suggest peak fall spawning ends by about late October. No abundant, distinct groups of fish 30–60 mm and 1.5–3 months of age originated during any late-fall or early-winter period studied (Fig. 4), although 30–75 mm fish—which we labeled Fall-spawned fish—persisted January through May in 1979 and 1980 and probably reflect some winter spawning.

Cohort spawning and recruitment periodicity vary within and between years. $Winter_{78}$ fish appeared as an abundant, distinct group in mid-April, but few recruited thereafter (Fig. 4). In contrast, $Winter_{79}$ and $_{80}$ fish did not form abundant, distinct groups until June, although a few fish appeared in May. Fall groups first appeared mid-November to early December. However, the bimodal size frequencies of the $Fall_{79}$ cohort in the period mid-February to early June 1980 suggest intragroup variation in spawning or recruitment success and periodicity similar to that for winter cohorts. We have interpreted the lower mode

of the $Fall_{79}$ cohort as actually being part of that cohort; the lower mode first became distinct in February 1980 when those fish were primarily 55–75 mm long and about 4 months of age, which would suggest early October to early November hatching.

Recruitment, movements, and nurseries

Fall cohorts of *P. burti* seemingly recruit in abundance at an older age (4–5 months) than Winter fish (2–4 months) off Texas. Winter fish formed abundant, distinct groups soon after first appearing mid-April to early June at 30–75 mm in length when 1.5–4.5 months old (Fig. 4). Fall fish did not form abundant, distinct groups until winter to early spring, although they first appeared mid-November to early December when 30–75 mm and 1.5–4.5 months old.

Young *P. burti* recruit to the bottom off Texas primarily in 5–27 m depths when 2–5 months old. $Winter_{79}$ fish 2–4 months old and 35–70 mm were captured only at 22 m in May 1979 (Figs. 4, 6). They occurred from 16–55 m during the period June through August 1979 (primarily June) but were most abundant at 22–27 m; few were shallower than 22 m or deeper than 36 m. Recently hatched $Fall_{79}$ fish 25–70 mm long were captured only at 5–9 m in mid-November 1979 (Figs. 4, 6). $Fall_{79}$ fish occurred only at 5–27 m (primarily 22–27 m) December 1979 through February 1980 when 3–5 months old. Similarly, $Fall_{78}$ fish were abundant at 5–27 m March through May when 7–9 months old, but few occurred in deeper water.

Juvenile *P. burti* disperse offshore as they mature and approach age I. $Winter_{79}$ fish were most abundant at 13–27 m depths September through November 1979 when 6–8 months old (Fig. 6). However, none occurred shallower than 22 m December 1979 through February 1980, when they were 9–11 months old; most were at 36–100 m. The largest $Fall_{79}$ individuals occurred in the deepest water December 1979 through February 1980, the size gradient suggesting gradual movement offshore. $Fall_{78}$ fish were almost exclusively at 5–27 m from March through May 1979 when 7–9 months old, but they were at 36–100 m from June through August when 10–12 months old.

Age determination using otoliths

Whole otoliths of *P. burti* apparently cannot be readily aged. Only 984 of 2461 whole otoliths examined had apparent internal features. Many were entirely opaque or lacked a distinct boundary between opaque and hyaline zones, possibly due to initial preservation or storage fluids, though fresh otoliths showed similar features. Only 11 of the 984 legible otoliths had an apparent annulus. These 11 fish were 120–160 mm in length and could have been about age I by length-frequency analysis. Annuli frequently were not apparent for fish that were age I by length frequencies.

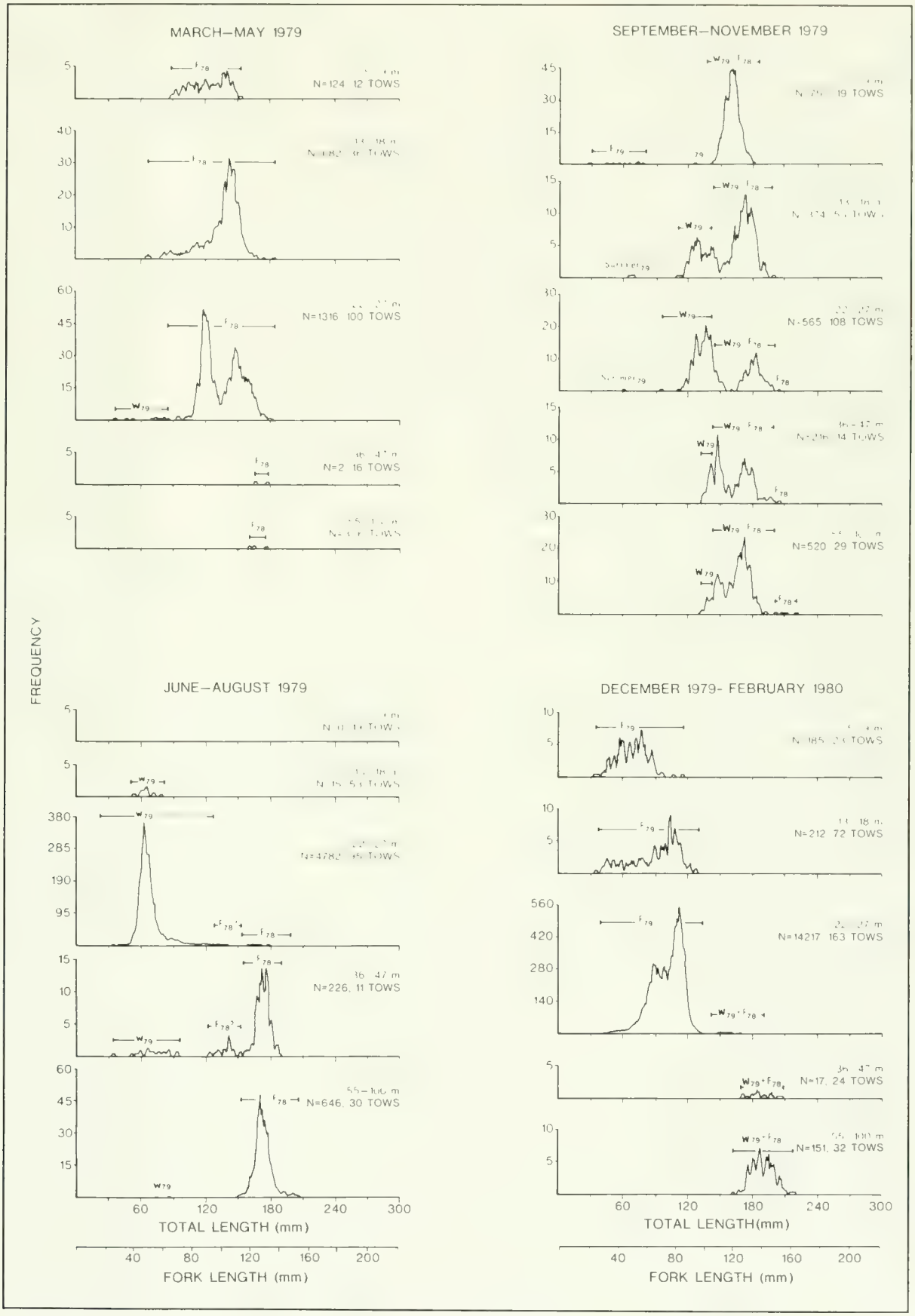
Growth and age determination by length frequency

Length frequencies could be used to determine age of *P. burti* through at least 13–16 months of age in the northwestern Gulf and apparently 20–27 months of age in the northcentral Gulf. No more than two cohorts occurred off Texas in any one month, except in March and December 1978, November 1979 through January 1980, and May through June 1980 when a few members of a third group were present (Fig. 4). Each cohort was followed easily until it disappeared when 13–16 months old. In contrast, in the northcentral Gulf in April 1980 there were three cohorts west of the Mississippi River and four to the east (Fig. 7). Fish were abundant at 20 months of age west of the Mississippi and were as old as 27 months to the east (Table 3).

Early sizes for *P. burti* average 25 mm in length at 1 month of age, 42 mm at 2 months, 57 mm at 3 months, 72 mm at 4 months, and 84 mm at 5 months. These values are predicted from quadratic regressions of length-on-age in days pooling all Winter and Fall cohorts (Table 2). Similar size-age combinations may be predicted from quadratic regressions for individual cohorts, and for pooled Winter groups and pooled Fall groups.

Peprilus burti average about 65–100 mm in length at 6 months, 120–145 at age I, and about 170 mm at age II, but fish in the northcentral Gulf were smaller at age than off Texas. Quadratic and von Bertalanffy growth equations both fit observed data from off Texas well, and they predict similar sizes-at-age over most of the observed size range (Fig. 8). For Winter fish quadratic and von Bertalanffy equations predicted lengths of 99 and 100 mm at 6 months, respectively, and 146 and 141 mm at age I (Fig. 8). Observed lengths show many Winter fish were as large as 120 mm at 6 months and 155 mm at age I (Fig. 4; Murphy 1981, Table 1). For Fall fish, quadratic and von Bertalanffy equations predict lengths of 93 and 97 mm at 6 months, respectively, and 131 and 130 mm at age I. Observed lengths show many Fall fish were as large as 105 mm at 6 months and 145 mm at age I. Winter-spawned fish from the northcentral Gulf averaged 120–124 mm at

Figure 6 (facing page)
Length frequencies of *Peprilus burti* by depth: March–May 1979, June–August 1979, September–November 1979, December 1979–February 1980.


MARCH–MAY 1979
N=124 12 TOWS
N=1316 100 TOWS
N=2 16 TOWS
SEPTEMBER–NOVEMBER 1979
N=565 108 TOWS
N=520 29 TOWS
JUNE–AUGUST 1979
N=226, 11 TOWS
N=646, 30 TOWS
DECEMBER 1979- FEBRUARY 1980
N=212 72 TOWS
N=14217 163 TOWS
N=17, 24 TOWS
N=151, 32 TOWS
FREQUENCY
TOTAL LENGTH (mm)
FORK LENGTH (mm)
TOTAL LENGTH(mm)
FORK LENGTH (mm)

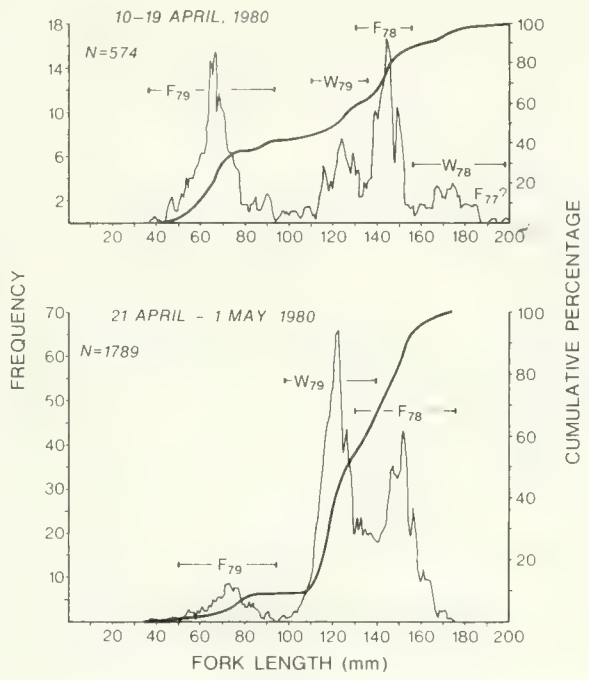


Figure 7

Length-frequency and cumulative percentages of *Peprilus burti* from the northcentral Gulf, (top) east and (bottom) west of the Mississippi River, April–May 1980. Cohort identities are indicated.

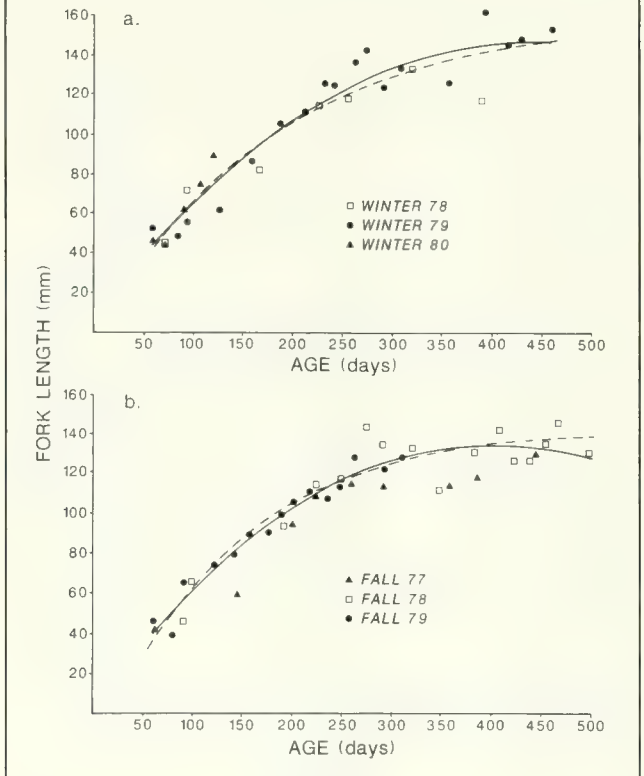


Figure 8

Mean observed and predicted sizes-at-age of Winter and Fall cohorts of *Peprilus burti* off Freeport, Texas. Predicted sizes were estimated for pooled Winter and Fall data from regressions of mean sizes-on-age using quadratic (solid line) and von Bertalanffy growth (dashed line) models. Regressions were significant at $\alpha = 0.05$.

13 months and 171mm at 27 months (Table 3). Fall-spawned fish averaged 66–73mm at 7 months and 142–149mm at 20 months.

Male and female *P. burti* reach a similar size off Texas. The largest male sexed was 173 mm and the largest female was 163mm. Both sexes were equally abundant among fish greater than 150mm.

Peprilus burti showed little apparent somatic growth off Texas as spawning approached, but fish from the northcentral Gulf had large annual growth increments. Off Texas, fish grew little after reaching modal sizes of 110–160mm at 7–15 months in Winter groups and 120–150mm at 9–16 months of age in Fall groups (Figs. 4, 8). Growth ceased or greatly slowed between

Table 3

Size-at-age (mm FL) data for *Peprilus burti* from the northcentral Gulf, east and west of the Mississippi River. Ages assume hatching dates assigned to cohorts off Freeport, Texas.

Spawned group	Approx. age (mo.)	West of Mississippi River			East of Mississippi River		
		n	Size range	Mean FL	*n*	Size range	Mean FL
$Fall_{79}$	7	150	50–95	73	235	37–93	66
$Fall_{78}$	20	743	132–176	149	196	130–155	142
$Fall_{77}$	33	0	–	–	0	–	–
$Winter_{79}$	13	1029	98–139	120	105	110–135	124
$Winter_{78}$	27	0	–	–	61	155–200	171
$Winter_{77}$	38	0	–	–	0	–	–

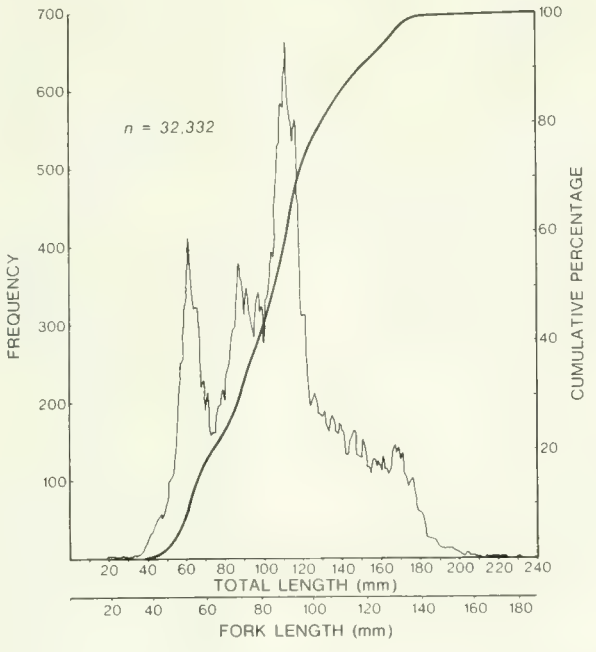


Figure 9
Length-frequency and cumulative percentage of *Peprilus burti* off Freeport, Texas.

the Late Developing and Ripe stages when sizes formed a plateau (Fig. 2). In contrast, growth of Winter and Fall cohorts in the northcentral Gulf continued for fish 7–13 months of age and 20–27 months of age (Table 3).

Maximum size and age

The maximum size of *P. burti* is about 200 mm in length. The largest of 32,332 fish we captured off Texas was only 180 mm, though a 198 mm specimen was measured among only 574 fish from the northcentral Gulf east of the Mississippi River (Fig. 7). Off Texas, 90% of the fish were less than 122 mm, 99% were less than 142 mm, and 99.5% were less than 145 mm (Fig. 9).

The maximum age of *P. burti* typically was only 1–1.5 years in the northwestern Gulf but appeared to be 2–2.5 years in the northcentral Gulf where the largest individuals occur. A t_L of 1–1.5 years seems reasonable off Texas, because fish larger than 142–145 mm, which made up less than 0.5–1.0% of the catch, approximate the average size there at age I. A larger t_L is appropriate for the northcentral Gulf (Fig. 7), because 99–99.5% of the fish west of the Mississippi River were less than 163–167 mm long and 99–99.5% of those to the east were less than 182–184 mm. These sizes approximate the average at age II in the northcentral Gulf and the oldest fish collected there was about age II, so a reasonable estimate of t_L is 2–2.5 years.

Total weight-length, girth-length, and length-length relationships

Regressions of total weight on fork length (Table 4) were significantly different (at $\alpha = 0.05$) in elevation between sexes ($F = 9.19$, 1, 1615 df) but not in slope ($F = 3.25$, 1, 1614 df). Calculated slopes did not significantly differ from $\beta = 3.0$ (males: $t = 0.97$, 789 df; females: $t = 1.60$, 825 df) except when all fish were pooled ($t = 20.08$, 2734 df). Girth-fork length and length-length regressions are in Table 4.

Table 4
Weight-length, girth-length, and total, fork, and standard length regressions for *Peprilus burti*. All regressions were significant at $\alpha = 0.05$. Measures are grams and millimeters.

Equation	*n*	FL range	r^2
$\log_{10}$ TW = −4.5517 + 2.9640 $\log_{10}$ FL (males)	791	100–163	0.89
$\log_{10}$ TW = −4.7095 + 3.0477 $\log_{10}$ FL (females)	827	94–164	0.93
$\log_{10}$ TW = −4.8621 + 3.1201 $\log_{10}$ FL (males, females, immatures)	2736	25–164	0.99
G = 10.38 + 0.99 FL	2736	25–164	0.95
FL = −4.31 + 0.96 G	2736	25–164	0.95
FL = 8.35 + 0.73 TL	2662	25–164	0.99
TL = −9.35 + 1.35 FL	2662	26–164	0.99
SL = 3.22 + 0.69 TL	2668	25–164	0.99
TL = −2.88 + 1.42 SL	2668	25–164	0.99
FL = 5.05 + 1.05 SL	2734	25–164	0.99
SL = −4.46 + 0.95 FL	2734	25–164	0.99

Discussion

Spawning periodicity and its regulation

The broad primary spawning period of September through May we suggest for *Peprilus burti* is realistic. Our data agrees with reports of fish 20–40 mm in length from December through June (Gunter 1945, Hoese 1965, Miller 1965) and, in part, with a suggested fall and winter spawning (Miller 1965). Moreover, Finucane et al. (1979) collected larvae off Texas from September through May.

We interpret our data to mean *P. burti* spawns primarily—or most successfully—in temporally separate, discrete, Winter (late January–mid-May), and Fall (early September–late October) periods. The consistently well-separated, bimodal length frequencies—on which we place great emphasis—must reflect a temporal separation in spawning activity or success, or growth and mortality, that originates during late fall and early winter. However, the well-developed gonads and Gravid/Ripe fish we observed suggest spawning could occur throughout that period, possibly at a low level. Allen et al. (1986) and Vecchione (1987) also found consistently bimodal size distributions of *P. burti* in the northcentral Gulf. Allen et al. (1986) considered them separate spawning peaks in a continuous, not temporally separated, spawning. The actual degree of temporal separation in spawning of *P. burti* may be important to resolve, because it may influence (1) appropriate management practices, (2) how many populations and stocks exist in *P. burti*, concepts which are not necessarily the same, and (3) how speciation occurs in *Peprilus*. Given properly randomized geographical sampling, age determination by daily otolith increments (Jones 1986) might resolve the question of how intense is late-fall to early-winter spawning and whether or not, and to what degree, spawning is temporally separate.

Although *P. burti* appear to spawn primarily in two main periods, Winter and Fall, it also appears that in each period there is much variation in cohort spawning periodicity or success, or in recruitment periodicity. We observed Winter cohorts to appear as distinct abundant groups in April in one year but not until June in two other years. Similarly, one Fall cohort was distinctly bimodal over a several-month time period. A more exact method of age determination than length frequencies, however, is needed to more clearly interpret these phenomena.

Our interpretation of spawning periodicity in *P. burti* is similar to findings that other Gulf species spawn in discrete Winter–Spring and Late Summer–Fall periods related to current transport, including *Cynoscion arenarius* (Shlossman and Chittenden 1981), *C. nothus* (DeVries and Chittenden 1982), *Larimus fasciatus* (Standard and Chittenden 1984), *Menticirrhus americanus* (Harding and Chittenden 1987), and *Polydactylus octonemus* (Dentzau and Chittenden 1990). Spawning of *P. burti* in the northwestern Gulf, and for many of these other fishes, probably is timed to coincide with currents (Shlossman and Chittenden 1981) that transport eggs and larvae from spawning areas to nurseries, assuming *P. burti* has pelagic eggs and larvae like *P. alepidotus* and *P. triacanthus* (Martin and Drewry 1978). Spawning, or its absence, coincides with wind-induced, up- or downcoast, alongshore coastal currents which drive circulation in the northwestern Gulf with seasonal reinforcement from the Mississippi—Atchafalaya discharge (Kelly et al. 1981). Average winds are downcoast (toward Mexico) during August/September–April/May but upcoast (toward Florida) during May/June–July/August. Nearshore currents parallel the coast. Upcoast wind stress causes upcoast alongshore currents which (1) are reflected in high inshore salinity off Galveston/Freeport and falling sea levels during early to midsummer (Marmer 1954, Kelly et al. 1981), and (2) coincide with the summer period of little spawning we observed in *P. burti* and which is reported in other species just cited. Downcoast wind stress causes downcoast (toward Mexico) alongshore currents, onshore surface Ekman transport, and downwelling which (1) are reflected in rising sea levels February–May and August–October, (2) transport low-salinity water downcoast causing a salinity minimum off Galveston/Freeport during September and October, and May and June, and (3) coincide with the two major spawning periods we suggest for *P. burti* and which are reported as major or minor periods in other species just cited. Alongshore currents continue downcoast from late fall to early winter. Seemingly, however, no distinct, abundant groups of *P. burti* originated then, which may reflect low-level spawning or spawning success. Similarly, little or no spawning occurs then in the other species just cited. Temporal variation in the average meteorological and hydrographic patterns may be the primary reason for the variation we noted in cohort spawning and recruitment periodicity between and within years.

Age determination and growth, maximum size and age, and mortality

Our findings on age and growth in *P. burti* are new, because this species has not been aged previously. It would be desirable to corroborate them by analysis of daily otolith increments (Jones 1986). However, that may not prove feasible, because recent studies using scales, opercula, vertebrae, and thin-sectioned otoliths, fail to consistently show clear daily increments or annuli (Allen et al. 1986). Therefore, it appears length frequencies are the only way to age *P. burti* at present. As in our study, supporting length collections must be frequent in time and over a long duration, because cohort boundaries and age are not clear every month. However, they are quite clear in certain months (for examples, the Winter$_{79}$ and $_{80}$ groups in May or June 1979 and 1980, the Fall$_{78}$ and $_{79}$ groups in December 1978 and 1979). From the clear groups, one can work chronologically backward and forward in time and gradually assign age and cohort boundaries with reasonable certainty. This process, however, is not as

simple in species with a complex life history like *P. burti* as it is in species that spawn during one major period a year.

The apparent cessation of somatic growth as *P. burti* approach spawning in the northwestern Gulf contrasts with large annual increments in the northcentral Gulf. This difference, combined with their disappearance from the northwestern Gulf at 13–16 months of age and their smaller maximum sizes and younger maximum ages there (see below), indicate fish from the northwestern Gulf (1) spawn and die at age I, or more probably (2) in some presently unclear combination emigrate offshore and to the northcentral Gulf prior to, or immediately after, spawning.

Few *P. burti* apparently exist larger than 190–200 mm in length. The largest we captured (180 mm, Texas; 198 mm, northcentral Gulf) are similar to maxima in other studies' sampling to at least 80–100 m depths (173 mm, Hildebrand 1954; 184 mm, Franks et al. 1972; 169 mm, Chittenden and McEachran 1976; 193 mm, Allen et al. 1986). Maxima are even smaller from estuaries or the shallow Gulf (154 mm, Gunter 1945; 131 mm, Miller 1965; 122 mm, Perret et al. 1971; 133 mm, Christmas and Waller 1973), which agrees with our findings that *P. burti* disperse to deep water as they mature. The largest records were from the northcentral Gulf (Allen et al. 1986; our study).

Our estimate that $t_L = 1–1.5$ years in the northwestern Gulf agrees with Chittenden and McEachran (1976) who suggested a 1–2 year maximum age. A higher t_L (2–2.5 years) in the northcentral Gulf appears realistic, because the largest records there are not much larger than the mean size at age II. Based on these maximum ages, theoretical estimates (Royce 1972, Hoenig 1983) of total annual mortality rate (1 – S) are nearly 100% in the northwestern Gulf and 82–90% in the northcentral Gulf. Murphy (1981) calculated similar values of 1 – S for the northwestern Gulf (99%) from observed time-specific abundance data for consecutive Winter or Fall cohorts. If mature fish from the northwestern Gulf emigrate offshore and to the northcentral Gulf, as we suggest, our values for maximum age and total mortality are under- and overestimates, respectively, for *P. burti* in the northwestern Gulf.

The presence of the largest *P. burti* in the northcentral Gulf follows a pattern in other marine and estuarine, demersal and pelagic species (*Cynoscion nothus*, DeVries and Chittenden 1982; *Stenotomus caprinus*, Geoghegan and Chittenden 1982; *Micropogonias undulatus*, Rivas and Rothmayr 1970, Gutherz et al. 1975, White and Chittenden 1977; *Brevoortia patronus*, Nicholson 1978; *Larimus fasciatus*, Standard and Chittenden 1984; and probably *C. arenarius*, Shlossman and Chittenden 1981). Small differences between areas also exist in other population attributes of *P. burti*, as in *C. nothus* and *L. fasciatus*: younger age compositions and maximum ages, smaller maximum sizes, and higher total annual mortality rates occur in the northwestern Gulf. At least three explanations could account for this: (1) There may be no basic differences between areas, just much greater biomass (Moore et al. 1970) at age in the northcentral Gulf; (2) differences may be real, not related to biomass, implying slight, but fundamental, population dynamics differences between areas; and (3) differences reflect some presently unclear combination of an offshore and spawning or postspawning movement of older, larger fish from the northwestern to the northcentral Gulf. The first implies Chittenden and McEachran (1976) and Chittenden (1977) are correct that shrimp communities on the Gulf continental shelf have a common population dynamics pattern. The other explanations imply that their arguments need modification for slightly longer life spans and lower mortality rates in the northcentral Gulf, and that shrimp communities are a little more sensitive to fishing than Chittenden's (1977) simulations indicate.

Movements, recruitment, and spawning areas

Peprilus burti probably spawn offshore. We found fish congregate in 36–100 m depths as they mature and size gradients that indicate an offshore dispersal. In agreement, Allen et al. (1986) found a positive correlation between mean size and depth at 200–290 m. Finucane et al. (1979) collected larvae in water 22–182 m deep on the continental shelf off Texas. The young make their way inshore to 5–27 m depths off Freeport, Texas—the white shrimp community (Hildebrand 1954, Chittenden and McEachran 1976)—where they recruit to the bottom. At least two mechanisms could explain their arrival inshore. For one, Ekman surface transport, associated with prevailing downcoast alongshore currents in the spawning season, could, in theory, bring the young inshore. However, Dentzau and Chittenden (1990) rejected this idea. It implies fishes of the brown shrimp community would also recruit inshore, but, in actuality, there is a clear separation between the two communities (Chittenden and McEachran 1976). A more likely alternative, suggested for *Polydactylus octonemus* (Dentzau and Chittenden 1990), is based on the hydrography and cyclonic gyre of the northwestern Gulf (Kelly et al. 1981, 1983, 1984): The eastward counterflow of the gyre is diverted inshore at the Mississippi River delta and ultimately extends downcoast as an alongshore current. Members of the white shrimp community could spawn anywhere in this flow, in the offshore northeastward flowing arc or in the

alongshore southwestward flow: the young just need to be entrained in waters already in the white shrimp community, or enter them using the eastward counterflow, and be transported in a "downstream manner" (see next paragraph). This interpretation is similar to the current transport model Shaw et al. (1985) suggest for *B. patronus*.

Besides being offshore, spawning grounds for *P. burti* found off Texas may lie towards or in the northcentral Gulf. We suggest some unknown combination of offshore and spawning or postspawning movement to the northcentral Gulf explains between-area population dynamics differences. Such upcoast movement may be required within the white shrimp community, given the coincidence of spawning with downcoast currents. Mean alongshore surface current speed is 23 cm/second in water 22 m deep off Freeport, Texas from September through June (Kelly et al. 1981), so spawning areas could lie 320 nmi upcoast assuming passive transport for 30 days before the young recruit to the bottom. This estimate depends on many poorly known factors, including (1) routes followed, (2) alongshore current speeds, (3) duration of the transport period, and (4) behavior of the young. However, alongshore currents could transport young great distances—conceptually "downstream"—and Texas recruits could be spawned off Louisiana where low-salinity waters propagate along Texas when alongshore wind components turn downcoast during August and September (Kelly and Randall 1980, Kelly et al. 1981). Mature fish must move toward spawning areas, conceptually in an upstream, contranatant direction from the northwestern Gulf, to maintain a fixed, proven spawning ground following Harden Jones (1968).

Zoogeographic considerations

Peprilus burti fill a niche in the Gulf similar to the one *P. triacanthus* occupies on the Atlantic coast. However, their population dynamics differ, and this may reflect zoogeographic variation suggested for other taxa whose ranges traverse the Cape Hatteras area, including *Micropogonias* and *Alosa* (White and Chittenden 1977), *Cynoscion* (Shlossman and Chittenden 1981), and *Stenotomus* (Geoghegan and Chittenden 1982). It appears for *P. burti* that (1) maturity occurs at 100–160 mm in length as they approach age I and spawn, (2) maximum size is only about 200 mm, but most are much smaller, (3) maximum age is no more than 2.5 years, and (4) total annual mortality rate is not lower than about 82%.

The life history of *P. triacanthus* north of Cape Hatteras is complicated by north–south and onshore–offshore movements (Horn 1970), but they appear to (1) mature at lengths of 110–130 mm in their second year (Hildebrand and Schroeder 1927, Bigelow and Schroeder 1953, Horn 1970, DuPaul and McEachran 1973), (2) reach maximum sizes of 300 mm (Murawski and Waring 1979), (3) have maximum ages of 3–6 years (Draganik and Zukowski 1966, DuPaul and McEachran 1973, Waring 1975, Kawahara 1977), and (4) have total annual mortalities of 67–84% (Murawski and Waring 1979).

Little has been published for *P. triacanthus* south of Cape Hatteras, but the largest fish collected in extensive trawling in this area was 150 mm (Wenner et al. 1979). This size range is more similar to *P. burti* than *P. triacanthus* north of Cape Hatteras and may reflect an intrageneric, Carolinian Province similarity in sizes, maximum ages, and mortality.

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Abstract.– Annual assessments of the Northwest Atlantic mackerel stock have occurred every year since 1973, providing useful advice to fishery managers involved in the decision making process for this important pelagic resource. Since 1985, assessment advice based on an $F_{0.1}$ management strategy has indicated that catches in the 300,000 mt range are feasible because stock biomass has increased greatly after the collapse of the fishery in the mid-1970s. However, indications from previous research are that compensatory processes are very important, so a stochastic simulation model with density-dependent growth, maturity, and natural mortality was constructed to study how these mechanisms might affect our ability to provide short- and long-term advice for this important stock. Model results suggest that our present assessments may be too optimistic relative to yield projections and that minimum spawning-stock biomass levels may be difficult to maintain even with an $F_{0.1}$ fishing strategy. Model results also reveal that natural mortality rates are probably much higher than previously thought and are important in determining trends in abundance in this stock.

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Impact of Compensatory Responses on Assessment Advice for the Northwest Atlantic Mackerel Stock

William J. Overholtz
Steven A. Murawski
William L. Michaels

Woods Hole Laboratory, Northeast Fisheries Science Center
National Marine Fisheries Service, NOAA, Woods Hole, Massachusetts 02543

The Northwest Atlantic stock of Atlantic mackerel *Scomber scombrus* has historically been important to the U.S. domestic fishery; records from the early 1800s to the 1980s suggest that cumulative landings have been 7–8 million mt over that time-period (Sette and Needler 1934, Hoy and Clark 1967, Anderson 1985). A thriving domestic industry utilized mackerel well into the 1940s until landings dropped because of declines in abundance, availability, and increased production of fresh and frozen white fish products (e.g., haddock, cod) (Hoy and Clark 1967, Jenson 1967). A resurgence of the fishery occurred in the 1970s when distant water fleets from eastern Europe and the Soviet Union landed an average of 310,000 mt annually from 1970 to 1976 (Fig. 1A). Since many of the important groundfish species in the region have declined recently, the U.S. industry has become more interested in mackerel as a volume (high-catch, low-price) fishery.

The fishery has been managed under the auspices of the Mid-Atlantic Fishery Management Council since 1977. Current management objectives for this stock include maintenance of a minimum spawning stock (600,000 mt), annual quotas based on an $F_{0.1}$ catch strategy and a recognition of the necessity for keeping the total stock at some reasonably high level to insure that the recreational fishery remains viable.

Recent assessments suggest that the stock has increased since collapsing in the late 1970s. A succession of moderate to good year-classes from 1981 to 1985 promoted rapid recovery of the stock to levels observed in the early 1970s (Fig. 1B, C). Assessment advice during the last several years based on an $F_{0.1}$ management strategy has indicated that annual catches in the 300,000 mt range are feasible in the short term. Allocations to joint ventures have increased over the last several years, amounting to about 75,000 mt in 1987, but recent landings have remained well below the 300,000 mt level and fishing mortality has averaged only about 0.07 since 1980 (Overholtz and Parry 1985).

Pelagic fishes such as mackerel are important in the trophic dynamics of fishery ecosystems, supporting populations of predatory fish, birds, and marine mammals. Additionally, these species may also increase to densities that inhibit their own population processes (e.g., growth, reproduction) and those of competitors. Evidence exists that Atlantic mackerel exhibit density-dependent growth (McKay 1979, Lett 1980, Overholtz 1989). Other factors such as maturation rates, fecundity-at-age, and predation mortality rates may also vary

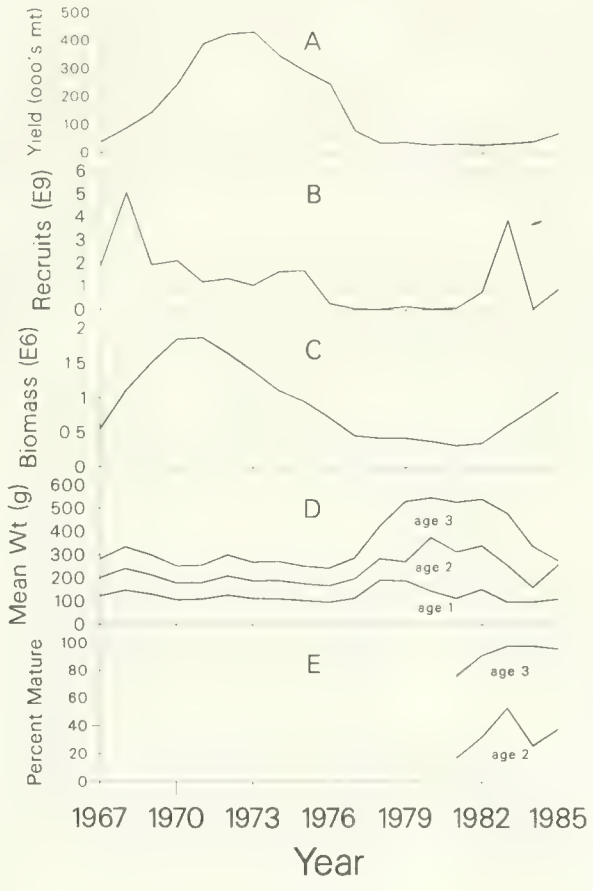

Figure 1

Descriptive data for the Northwest Atlantic mackerel stock, 1967–85. (A) Yield (ooo's mt); (B) Recruitment at age 1 (billions of fish); (C) Spawning-stock biomass (ooo's mt); (D) Mean weight at ages 1, 2, and 3 from commercial samples (g); (E) Percent maturity for ages 2 and 3.

with stock size. An analysis of the food habits of mackerel predators suggested that natural mortality rates (M2) for this stock were higher during 1973–75 when relatively large numbers of juvenile mackerel were available, and declined during 1976–80 when there were few small fish (NEFC 1987).

This study examines the impact that compensatory changes in growth, sexual maturity, and natural mortality rates may have on the Northwest Atlantic mackerel stock. Implications of responses in these factors on catch and spawning-stock biomass are evaluated using a simulation model. The model was designed so that changes in these compensatory factors as well as the influence of fishing mortality patterns and strategies could be assessed.

Model background

Data on potential density-dependent population regulatory mechanisms were obtained from research vessel survey cruises and commercial fishing operations conducted on the U.S. eastern coast. Information from spring groundfish surveys conducted by the Northeast Fisheries Center (NEFC) during 1973–85 and a commercial fishery conducted by Poland during 1981–86 were examined to quantify compensatory relationships. Analyses were performed to study changes in growth, maturation rates, and natural mortality (Overholtz et al. 1988, Overholtz 1989).

Significant negative relationships between mean weight-at-age and stock size were confirmed for both research and commercial data sources (Overholtz et al. 1988, Overholtz 1989). Mean size-at-age for recent year-classes was also found to be significantly different; large year-classes grew more slowly (Overholtz 1989). In addition mean weight-at-age was also negatively related to year-class size, indicating that large cohorts may depress growth rates of individuals from that particular year (Overholtz 1989) (Fig. 1D). These analyses helped us to quantify the relationship between growth and density for this stock in our modeling exercises.

Maturity data from 1981–86 were evaluated to ascertain if percent maturity at age 2 and 3 changed over the time period. No fish were mature at age 1, and all fish were mature at age 4+ (Overholtz et al. 1988). Percent maturity at age 2 ranged from 17% in 1981 to 53% in 1983 (Fig. 1E). Percent mature at age 3 ranged from 67% in 1986 to 98% in 1983 and 1984 (Overholtz et al. 1988) (Fig. 1E).

The maturity data were collected in conjunction with age sampling and were not a priority item. During the critical time of gonadal development in mid- to late April, maturity samples were often sparse because age sampling requirements had been fulfilled; no additional maturity samples were collected because of this. A cursory examination of the data revealed that there was an apparent negative relationship with increased stock size at age 2 and no consistent pattern at age 3 (Overholtz et al. 1988) (Fig. 1). The null hypothesis of no impact of density on maturity rates could not be accepted or rejected with the data at hand; we therefore included this potential mechanism in our modeling studies to ascertain its overall importance.

During 1967–85 the northwest Atlantic mackerel stock underwent profound changes in recruitment with a subsequent decline in biomass (Fig. 1B, C). We considered this a good time period to study changes in predation on mackerel and associated possible changes in natural mortality rates (M). For the purposes of discussion in this paper we define natural mortality rate (M = M1 + M2), where M1 = sources of natural mortal-

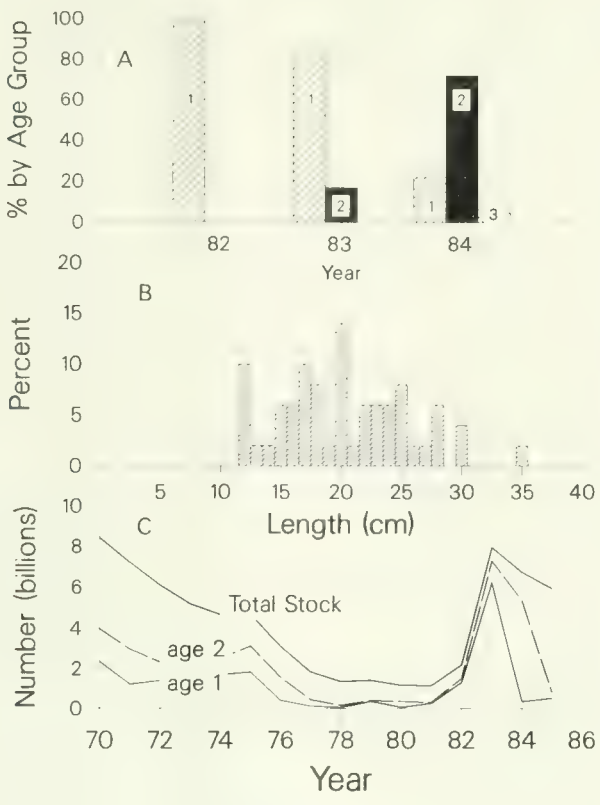

Figure 2

(A) Percent by age group of Atlantic mackerel sampled as prey in Atlantic cod, silver hake, and spiny dogfish stomachs in 1982 (n = 8), 1983 (n = 12), 1984 (n = 32). (B) Length frequency of mackerel sampled in Atlantic cod, silver hake, and spiny dogfish stomachs, 1982–84. (C) Cumulative numbers of ages 1 and 2, and the total stock of mackerel from VPA stock size estimates for 1970–85.

Table 1

Percentage of mackerel by weight in stomach samples of silver hake, Atlantic cod, and spiny dogfish, and number of stomachs collected for 1973–76 and 1977–80.

	1973–76		1977–80	
Species	%	N	%	N
Silver hake	4.21	2622	0.82	1657
Cod	11.50	1009	0.10	457
Spiny dogfish	3.30	389	0.10	2662

ity other than predation, and M2 = predation mortality (ICES 1987). Since there was no multispecies virtual population analysis (MSVPA) available to examine annual trends in predation mortality rates (M2), we decided to use another method to examine possible changes in M2. We wanted to investigate possible predation mortality models for mackerel for this period of time.

Summaries of NEFC food habits data indicate that spiny dogfish *Squalus acanthias*, Atlantic cod *Gadus moruha*, and silver hake *Merluccius bilinearis* are the most important fish predators on mackerel (Langton and Bowman 1980, Bowman and Michaels 1984, Bowman et al. 1984). Food habits data were collected from 1973 to 1980, but did not include individual lengths of prey items from these predators. However, maximum, minimum, and average lengths of fish prey were recorded. Almost all the mackerel consumed in these years were less than 30 cm (Overholtz et al. 1988).

To study the problem in more detail, food habits data from 1982–84 were examined to determine the size and age distribution of mackerel as prey items in the three fish predators. These data were chosen since detailed records of predator and prey length were available. Mackerel up to 35 cm were taken as prey by the three species, but fish 30 cm or less composed the bulk of the prey. These fish were predominantly ages 1 and 2 from the 1981–83 year-classes (Fig. 2A, B). Mackerel appeared to be consumed roughly in proportion to their abundance in the sea during 1982–84 (Fig. 2A, C).

Our analysis thus centered on predation by these three predators on age-1 and -2 mackerel. Total food consumed (all species) by each predator was calculated and the average percentage of mackerel by weight comprising the diet of each predator was estimated separately for the periods 1973–76 and 1977–80 (Table 1). A period average was used because there was not enough information available for annual estimates. These two time-periods were chosen because the design of the food-habits sampling regime was different in each period, and because the abundance of small mackerel was much different in each of the periods (Fig. 2C).

The method used to calculate consumption was based on residence times of the predator and prey, percent by weight of mackerel in the predator diet, daily ration estimates for the predator by season, if available, abundance of 1- and 2-year-old mackerel in the sea, and biomass of predators of the correct size distribution (Bowman et al. 1984, Rexstad and Pikitch 1986). This method assumed that the estimate of predator biomass was an appropriate measure of the average standing stock present during the year, that mackerel consumed were only age-1 and -2 fish, and that predators consumed mackerel relative to their abundance in the sea. The estimates were made for 1973–80 for each predator species and the total number of age 1- and -2 fish consumed annually was estimated (Table 2).

Total consumption of mackerel by each predator was calculated as

$$C_i = B_i \cdot \%BW \cdot \%Rm_i \cdot Tr \quad (1)$$

where

C_i = consumption of mackerel by predator i,
B_i = biomass of predator i,
%BW = daily ration estimate,
%Rm = percent of total ration composed of mackerel for predator i,
Tr = residence time of predator and prey (days), and
i = 1,3.

The estimated consumption in weight was then converted to numbers eaten on the basis of information on the abundance of age-1 and -2 mackerel in the sea and the mean weights of each age group. Consumption estimates were combined with landings-at-age for 1973–80 and a new VPA was completed for these years (Overholtz et al. 1988). A residual natural mortality rate (M1) of 0.20 was used in this analysis to account for other sources of mortality at ages 1 and 2 and for all the other age groups (3–14) in the analysis. A similar assumption has been used by ICES in the multispecies VPA model of the North Sea (ICES 1987). The mortality rates from the VPA were a proxy for F and M2 and were apportioned by using the ratios of consumption and landings to total deaths (numbers). This gave an estimate of F and M2 mortalities for 1973–80 (Table 3). Consumption (numbers) of age-1 mackerel exceeded landings of that age group in all years from 1973 to 1980 and was generally smaller than landings at age 2 (Table 2). Sizes of incoming year-classes increased up to a factor of two in the revised VPA over the 1973–80 period (Overholtz et al. 1988). When mortality rates from the VPA were apportioned by consumption estimates and landings, natural mortality rates (M = M1 + M2) were generally higher in the 1973–76 period, when mackerel were abundant, than in 1977–80 (Table 3).

These values and the new VPA stock size-at-age estimates were used in regressions to study the relationship between M2 and year-class strength. The results of this analysis suggest a positive relationship between M2 for ages 1 and 2 and year-class size (R = 0.37, 0.78, P = 0.363, 0.0234), respectively (Fig. 3A, B). An examination of the scatter plots from these two regressions revealed that the M2 value from 1976 was high relative to the number of age-1 and -2 fish in the stock. There were fewer age-1 fish in the stock in 1976 (Fig. 2C); furthermore, food habits data indicated that mackerel was not present in the diet of the three predators in 1976. The 1976 data point was dropped and a new regression was fitted for age 1 (R = 0.60, P = 0.157, Fig. 3A).

We were cognizant of the fact that results of this analysis may have been influenced by the assumption of proportional feeding. However, the suggestion that natural mortality rates may change with year-class size is an interesting research question. A positive relationship between year-class size and predation mortality rate has obvious implications for assessment and management, and thus the potential impacts of density-dependent predation mortality were a major focus of our modeling studies.

Table 2
Annual consumption of age-1 and -2 Atlantic mackerel by spiny dogfish, silver hake, and Atlantic cod, landings of mackerel for 1973–80, and total for both categories (millions of fish).

	Consumption		Landings		Total	
Year	Age 1	Age 2	Age 1	Age 2	Age 1	Age 2
1973	590.0	224.1	161.8	283.2	751.8	507.3
1974	823.0	135.1	95.9	242.2	918.9	377.3
1975	616.0	170.0	373.7	431.4	989.7	601.4
1976	202.8	278.3	12.5	353.5	215.3	631.8
1977	8.4	15.1	2.0	27.0	10.4	42.1
1978	11.1	6.6	0.1	0.2	11.2	6.8
1979	14.1	1.2	0.4	0.6	14.5	1.8
1980	6.1	8.4	1.2	10.9	7.3	19.3

Table 3
Mortality rates of age-1 and -2 Atlantic mackerel for 1973–80.

	Age 1				Age 2			
Year	Z	F	M2	M1	Z	F	M2	M1
1973	0.78	0.12	0.46	0.20	0.75	0.31	0.24	0.20
1974	0.66	0.05	0.41	0.20	0.86	0.42	0.24	0.20
1975	0.71	0.19	0.32	0.20	0.83	0.45	0.18	0.20
1976	0.81	0.04	0.57	0.20	0.93	0.41	0.32	0.20
1977	0.40	0.04	0.16	0.20	0.42	0.14	0.08	0.20
1978	0.61	0.00	0.41	0.20	0.39	0.01	0.18	0.20
1979	0.30	0.00	0.10	0.20	0.31	0.04	0.07	0.20
1980	0.44	0.04	0.20	0.20	0.38	0.10	0.08	0.20

Model structure

A simulation model addressing changes in growth, percent maturity-at-age, and predation mortality rates

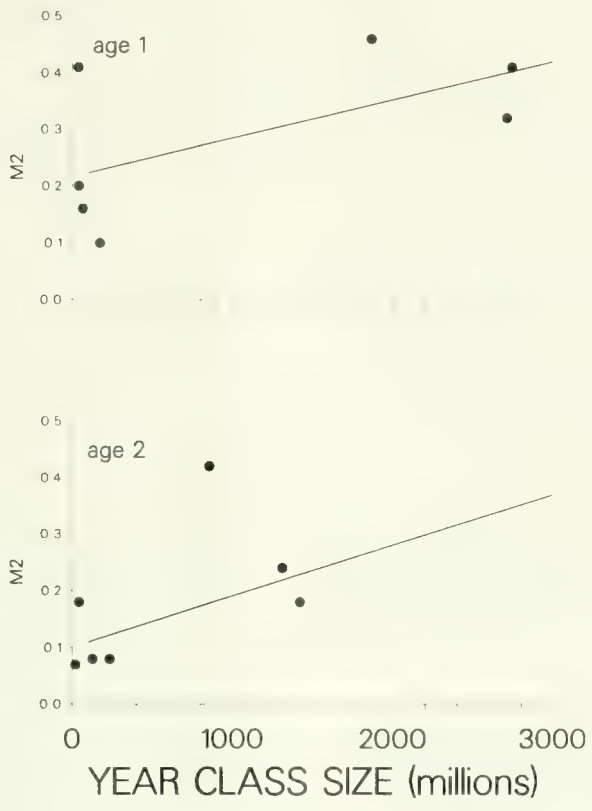

Figure 3
Relationship between predation mortality (M2) and year-class size for age-1 and -2 Atlantic mackerel from calculations of mackerel consumption by Atlantic cod, silver hake, and spiny dogfish for 1973–80.

(M2) was constructed to evaluate the potential impact of these population regulatory mechanisms in the context of single-species assessment advice. The model was a basic fishery simulator much in the same style as many other common fishery models (Walters 1969, Sissenwine 1977). An age-structured Baranov catch equation was used to compute annual fishery yields, and the negative exponential relationship was used to update stock size for 14 age groups.

A stochastic recruitment function was used to model recruitment for the mackerel stock. A three-parameter model (Shephard 1982; Table 4) with a lognormal white-noise multiplier was used to generate an annual estimate of recruitment as:

$$R = (a * SSB)/[1 + (SSB/K)^b] * lnm \quad (2)$$

where R = recruitment at age 1,
SSB = spawning-stock biomass,

Table 4
Parameters used in stochastic simulations of the Atlantic mackerel stock; e-4 = 10^{-4}, e-5 = 10^{-5}, e-6 = 10^{-6}.

	age	a	b	K
Weight (Wt_i)	1	0.122	-1.24e-5	—
Growth (G_i)	2	0.187	-1.42e-5	—
increment	3	0.154	-1.08e-5	—
	4	0.132	-1.03e-5	—
	5	0.102	-8.62e-6	—
Recruitment (R)	1	5.800	1.7	600.0
Maturity (PM)	2	0.543	-2.14e-4	—
	3	1.043	-2.14e-4	—
Predation	1	0.600	3.00	2.5
mortality (M2)	2	0.500	2.00	2.5

a, b, K = parameters,
lnm = lognormal multiplier with u and s from the SR data.

Recruitment estimates were scaled upward by a factor of 1.5 to account for the fact that the original VPA age-1 stock size estimates do not reflect higher natural mortality rates due to predation (Overholtz et al 1988).

Growth-at-age was based on a two-stage model that related life-history characteristics and year-class size to growth increment for a year-class (Overholtz 1989). Since age-1 fish maintain a separate distribution from the adult stock (Sette 1950) a relationship between age-1 growth and corresponding age-1 year-class size was used to predict weight at age 1. The relationship was parameterized (Table 4) with available empirical data, such that size at age 1 varied from 48 g for slow-growing fish to 122 g for fast-growing fish (Overholtz 1989). Weight of age-1 mackerel was calculated as

$$Wt_1 = a - bN_1 \quad (3)$$

where Wt = average weight (g) at age,
N_1 = year-class size at age 1 (numbers),
a, b = parameters.

Age 2–5 growth was determined by relationships between adult stock size (numbers) and growth-at-age (Table 4) calculated as

$$Wt_i = Wt_{i-1} + G_i \quad (4)$$

where Wt_i = average weight at age i, i = 2,5,
G_i = annual age-specific growth increment (g),

and

$$G_i = a_i - b_i SS \quad (5)$$

where SS = total adult stock size (numbers),
a,b = age specific parameters.

The increment from ages 2 to 5 was smaller the larger the adult stock. Fish weight at ages 1–5 was the result of growth in the first year and subsequent increments at ages 2–5; thus, age-1 growth partially determined the average weight of a fish throughout its lifetime. If the stock was reduced in any given year, the cohort could recover and grow faster. Growth at ages 6+ was assumed to follow trends in the recent data, since by this time cumulative mortality has usually been sufficient to reduce a cohort to lower levels.

Percent maturity at ages 2 and 3 was assumed to vary based on a relationship between the fraction mature and spawning stock size calculated as

$$PM_i = a - b(SSB) \quad (6)$$

where PM_i = percent mature at age i, i = 2,3,
SSB = spawning-stock biomass,
a,b = parameters.

This submodel was parameterized (Table 4) so that the maturity of age-2 fish can vary from 20 to 50%, while maturities for age-3 fish range from 70 to 100%.

Natural mortality due to predation (M2) for ages 1 and 2 fish was estimated from a relationship between M2 and year-class size-at-age (Fig. 4; Table 4) calculated as

$$M2_i = (a * YC_i)/[1 + (YC_i/K)^b] \quad (7)$$

where $M2_i$ = natural mortality due to predation on age i, i = 1,2,
YC_i = year-class size at age i, i = 1,2,
a,b,K = parameters.

M2 mortalities on age-1 and -2 fish could reach approximately 1.0 and 0.6, respectively, with this model.

This relationship was used since it approximates the findings of our mortality study over an initial range of stock size (Fig. 3A, B), and since it appears to be an appropriate predator prey response model (Holling 1965, Murdoch 1973). Although this model does not produce a typical type-3 response (Holling 1965) exactly, since there is no inflection point over the initial stock sizes (Fig. 4), it serves as a sufficient functional model to study the natural mortality mechanism.

The density-dependent simulation model (DDM) was used to study the impact of different levels of fishing mortality, management strategies, and to investigate hypotheses concerning the role of compensatory responses in regulating this stock. Monte Carlo simulations were produced for a variety of different scenarios, and average results from 1000 annual data points were summarized. Results from the model were compared with forecasts from the current standard assessment model (STD).

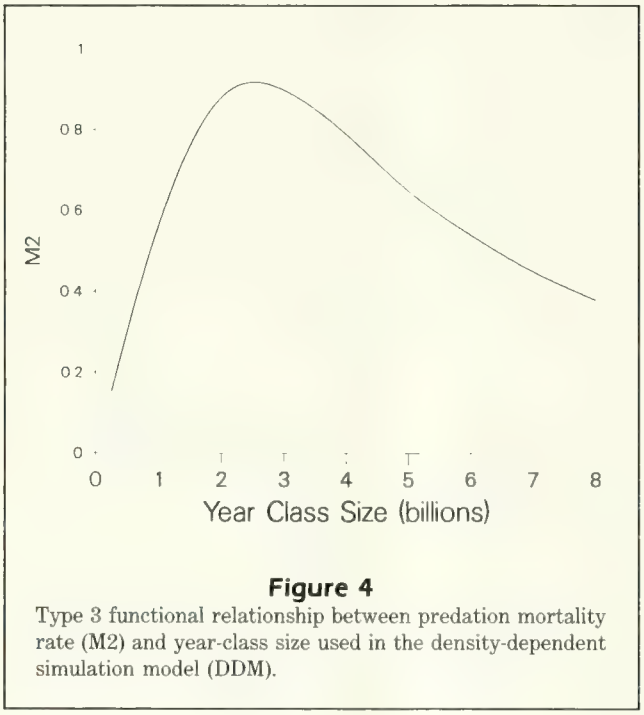

Figure 4
Type 3 functional relationship between predation mortality rate (M2) and year-class size used in the density-dependent simulation model (DDM).

Model sensitivity and validation

The sensitivity of model results to the different density-dependent mechanisms was investigated by comparing catch in 1987 and spawning stock in 1988 and 1991 for all the different combinations of growth, maturity, and natural mortality at a reference fishing mortality of 0.05. In runs where only a single mechanism was examined, 1987 catch was most affected by changes in the growth pattern (mean weights) of the stock (Fig. 5-B). Spawning stock in 1988, on the other hand, was almost equally sensitive to maturity and natural mortality. Density-dependent natural mortality influenced 1991 spawning stock to the greatest degree (Fig. 5-C).

When the results of pairing the mechanisms were examined, weight and natural mortality had the greatest effect on catch, percent maturity, and natural mortality on SSB in 1988 and weight and natural mortality on SSB in 1991 (Fig. 5-D, E, F). When the three mechanisms were all operating there was no change in the impact on 1987 catch, but spawning stock in 1988 and 1991 was several percentage points lower (Fig. 5-G).

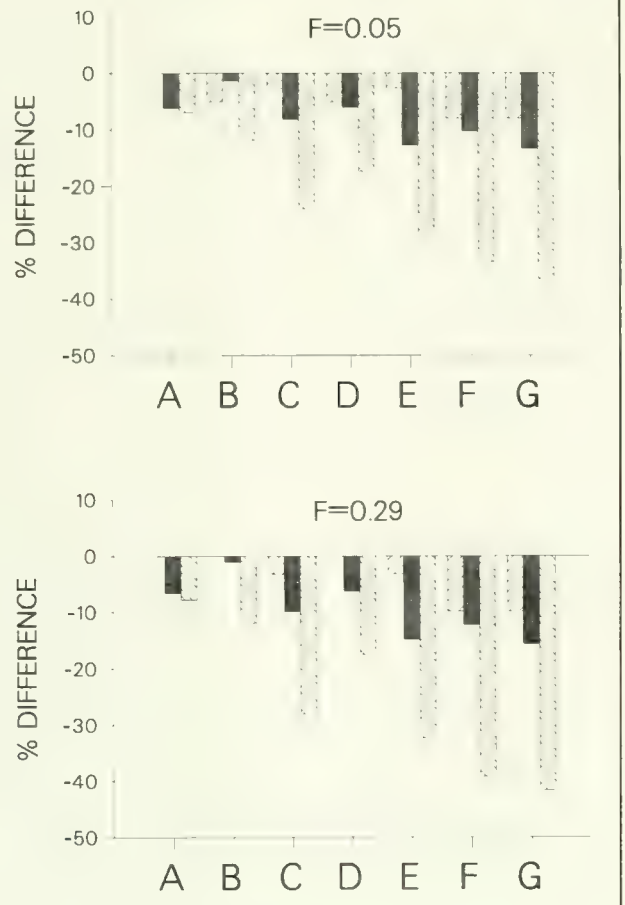

Figure 5

Impact on 1987 catch, 1988 spawning-stock biomass (SSB), and 1991 SSB of running the density-dependent simulation (DDM) model with all possible combinations of growth, maturity, and predation mortality. (A) maturity; (B) growth; (C) predation mortality; (D) growth, maturity; (E) maturity, predation mortality; (F) growth, predation mortality; (G) maturity, growth, predation mortality.

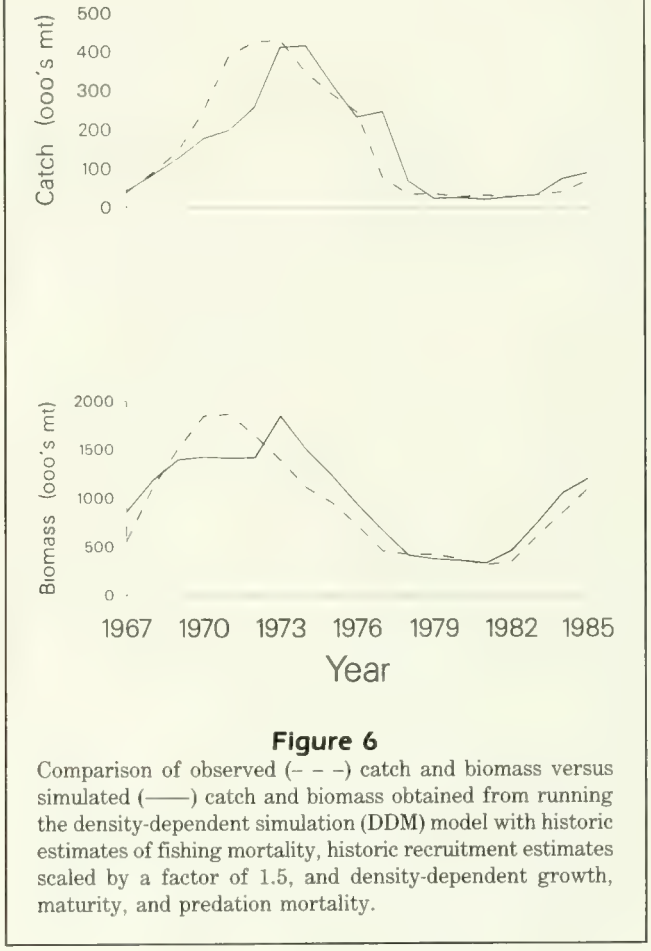

Figure 6

Comparison of observed (– – –) catch and biomass versus simulated (——) catch and biomass obtained from running the density-dependent simulation (DDM) model with historic estimates of fishing mortality, historic recruitment estimates scaled by a factor of 1.5, and density-dependent growth, maturity, and predation mortality.

A validation run of the density-dependent model was produced for comparison with the observed time-series of catch and VPA biomass for 1967–85 (Fig. 6). The simulated series was produced by using the same fishing mortality series as in the VPA, recruitment scaled upward by a factor of 1.5, and density-dependent growth, maturity, and natural mortality. The pattern of simulated versus observed catch and biomass is quite comparable in terms of trend and magnitude, except for a few years in the early 1970s. This occurs even though the density-dependent model has greatly different natural mortality rates at ages 1 and 2 and much higher recruitment. Another run with the same F pattern, recruitment scaled by 1.5, and no density dependence produced the same trend in catch and biomass for 1967–85, but the values were approximately a factor of two larger than the observed series. Thus, not including the density-dependent component resulted in values of catch and SSB that were greatly different than the observed series.

The model components were validated by comparing the different outputs produced by the various mechanisms with available empirical data. In some cases, relationships were re-parameterized or tuned to produce results in the same ranges as observed in the empirical database. The model was used to investigate a variety of different problems. Runs from the STD model were compared with the results of the different density-dependent model outputs to gauge the changes that occurred in catch, total stock, spawning stock, mean weights, and other factors. STD runs were parameterized with the same data as that used in the 1986 assessment (Overholtz et al 1988).

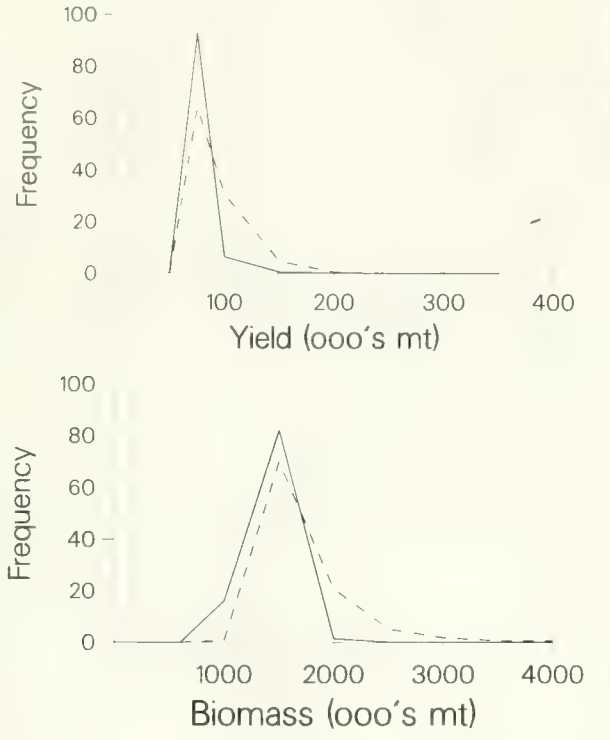

Figure 7
Comparison of standard assessment (STD) model (– – –) and density-dependent simulation (DDM) model (——) catch and spawning-stock biomass (SSB) for 5000 iterations of each model, with fishing mortality set at 0.05.

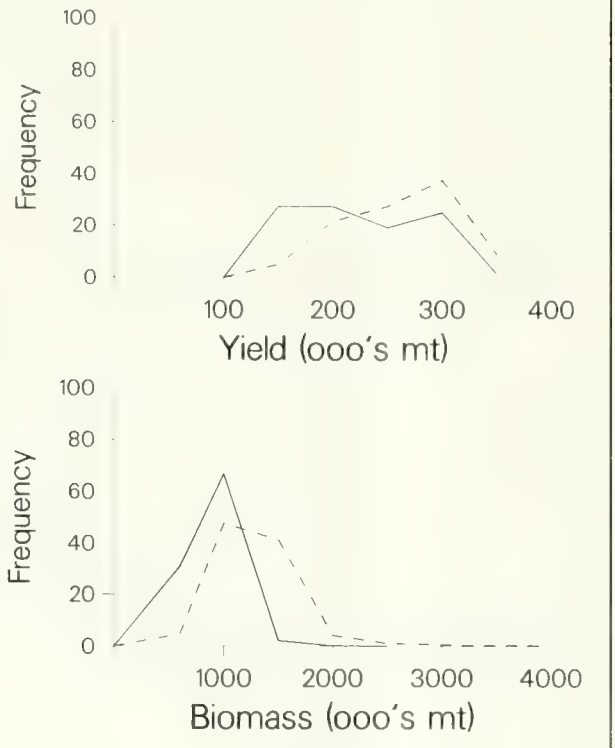

Figure 8
Comparison of standard assessment (STD) model (– – –) and density-dependent simulation (DDM) model (——) catch and spawning-stock biomass (SSB) for 5000 iterations of each model, with fishing mortality set at 0.29 ($F_{0.1}$).

Model results

Short-term perspective

Since fishing mortality has been so low in recent years and the stock has increased, an attempt was made to investigate the effect of further stockpiling of fish on expected catches and spawning stock size. To address this problem, a series of 5-year simulations were used to compare the density-dependent model results with projections from the standard model. Fishing mortality was set at 0.05, a value close to the average rate over the last several years. These runs suggest that advice based on the standard model would have overpredicted catch by about 8% in 1987 and spawning stock size in 1988 by about 13% (Fig. 5-G). Furthermore, if the standard model were used to project more than a few years into the future, the estimate of spawning stock could possibly be too large; the 1991 estimate would be lower by 37% for the DDM model (Fig. 5-G). If the frequency of yields over this 5-year series is calculated, the STD model is more optimistic with a mean catch of 74,892 mt versus 63,686 mt for the DDM model (Fig. 7). Similarly for spawning-stock biomass (SSB), the STD model suggests a higher mean SSB of 1.5 million mt versus 1.1 million mt for the DDM model (Fig. 7).

Since $F_{0.1}$ is an important benchmark fishing-mortality rate in the present management plan, another 5-year summary with $F = 0.29$ ($F_{0.1}$) was also produced. As with the previous example, mean yield for the STD model was considerably higher, 242,939 mt versus 197,116 mt for the DDM model (Fig. 8). Spawning-stock biomass would be considerably different under the two perspectives with an estimated mean SSB of 1.0 million mt under the STD model and 725,887 mt under the DDM model (Fig. 8).

Long-term perspective

To develop a longer-term perspective, simulations at the same two levels of fishing mortality ($F = 0.05, 0.29$) were produced for 15-year series to allow sufficient

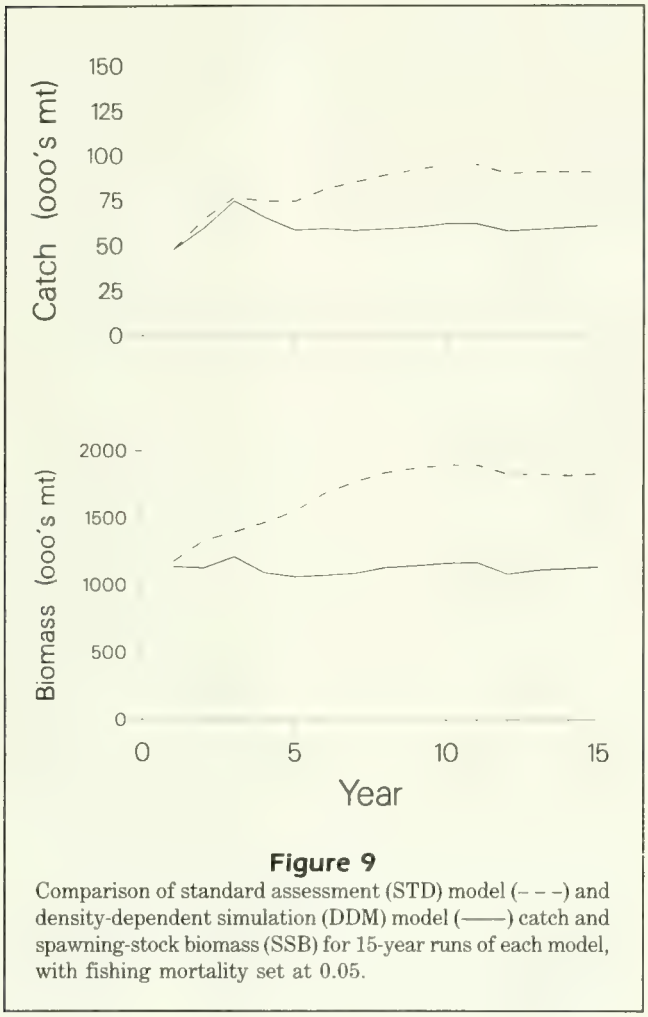

Figure 9
Comparison of standard assessment (STD) model (– – –) and density-dependent simulation (DDM) model (——) catch and spawning-stock biomass (SSB) for 15-year runs of each model, with fishing mortality set at 0.05.

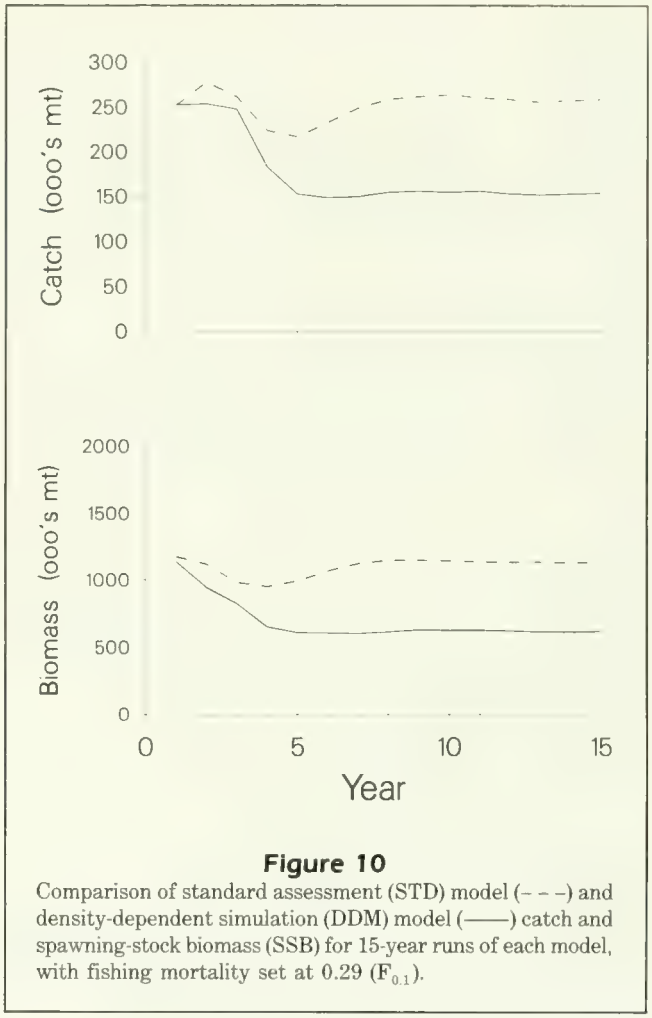

Figure 10
Comparison of standard assessment (STD) model (– – –) and density-dependent simulation (DDM) model (——) catch and spawning-stock biomass (SSB) for 15-year runs of each model, with fishing mortality set at 0.29 ($F_{0.1}$).

time for the stock to reach an equilibrium point. At F = 0.05, and after roughly 7–8 years, catch would be higher under the STD model than for the DDM model (Fig. 9). Spawning-stock biomass would also be considerably higher, about 1.7 million mt for the STD model versus about 1.1 million mt for the DDM model (Fig. 9).

Fishing the stock at $F_{0.1}$ for a 15-year period would result in an equilibrium catch of roughly 250,000 mt (STD) versus 150,000 mt (DDM) after about 7–8 years (Fig. 10). The spawning stock would appear to be much higher, 1.1 million mt versus 615,000 mt, for the STD and DDM models, respectively (Fig. 10).

To evaluate the overall differences between the two models, two measures of performance and one measure of risk were produced for fishing mortality values ranging from 0.1 to 0.6, in 0.1 increments for a total of 1000 runs of each model. Mean catch, coefficient of variation (CV) of catch, and proportion of time the spawning stock fell below 600,000 mt, the management plan benchmark, were calculated for year 10 of the simulation. Based on the previous model runs, the tenth year of the simulation appeared to be a reasonable choice for a summary year (Figs. 9, 10).

Mean catch would continue to increase dramatically under the STD model until F reached about 0.40 and would remain relatively constant thereafter. Yields would also steadily increase for the DDM model at F's ranging from 0.1 to 0.3, but would remain constant after that point (Fig. 11A). A comparison of expected yields under the two models suggests that the STD model is always more optimistic, especially at the higher levels of fishing mortality (Fig. 11). Mean catch at F = 0.5 would be about 125,000 mt higher under the STD model.

Variability as measured by CV's of the catch increased with increases in fishing mortality for the STD model, but remained relatively constant at about 50% for the DDM model. Thus the STD model is more optimistic at lower levels of fishing mortality and becomes

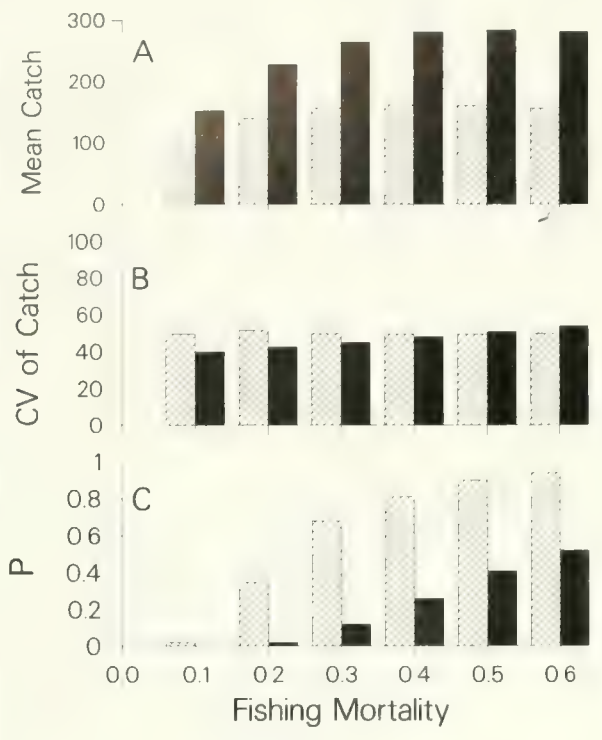

Figure 11

(A) Mean catch, (B) coefficient of variation of catch, and (C) proportion of the time spawning-stock biomass (SSB) falls below 600,000 mt for year 10 of a set of 10-year simulations of the standard assessment (STD) (darkened bar) and density-dependent simulation (DDM) (cross-hatched bar) models, with fishing mortalities of 0.1–0.6 in 0.1 increments.

progressively more variable as fishing mortality increases (Fig. 11B). Both models have relatively high CV's at all levels of fishing mortality, suggesting a large range in possible catches.

The minimum spawning-stock criteria of 600,000 mt is a threshold biomass defined in the present fishery management plan. This value was chosen by managers because a relatively clear demarcation point between low and high recruitment is evident in the 1962–85 stock-recruit data series (Anderson 1985). When the simulation results are expressed relative to the proportion of times the SSB drops below the 600,000 mt level for each model, the STD model appears to be much less prone to risk and, therefore, is much more optimistic than the DDM model results. The proportion ranges from 0.0 at F = 0.1 to about 0.52 at F = 0.6 for the STD model, while P ranges from 0.01 to 0.94 for the DDM model (Fig. 11C). The STD model results suggest that there is little risk of the SSB dropping below the threshold, even at fishing mortality rates of 0.4–0.5 (Fig. 11C). The DDM model results are much less optimistic, suggesting the need for some concern at fishing mortality levels of 0.3 and greater (Fig. 11C).

Discussion

Biological interactions may play an important role in regulating marine ecosystems (Sherman et al. 1981, Walters et al. 1986, Overholtz and Tyler 1986, Overholtz et al. In press). Species interactions are becoming an important fishery management issue, and assessment advice is increasingly contingent on these mechanisms (Anderson and Ursin 1977; Pope 1976, 1979; Shephard 1984; ICES 1987,1988). This study indicates that the stock dynamics of Atlantic mackerel are not only influenced by fishing, but that predation and intraspecific compensatory mechanisms including density-dependent growth are strong influences that probably effect yield forecasts and management advice in the short and long term.

Large differences in mackerel growth suggest that year-class size partially influences the initial pattern of growth during a cohort's first several years. Adult stock size probably plays an important role in regulating growth after a year-class recruits to the adult portion of the population (Overholtz 1989). Declines in growth are probably significant as stock biomass increases (Overholtz 1989). Model results, although not presented in this paper, suggest that mackerel would reach a larger size if the mackerel stock were fished more heavily. Larger catches of Atlantic mackerel would probably cause growth to stabilize at higher rates, and more of the annual production would be available for harvest.

Predation mortality rate has usually not been accounted for in the past in most assessment work, but recent studies have shown the importance of including this mechanism to enhance stock assessments (Anderson and Ursin 1977; Shephard 1984; ICES 1987,1988; Overholtz et al. 1990). Our analysis suggests that predation probably has a major influence on the dynamics of Northwest Atlantic mackerel. Predation mortality is probably the largest component of natural mortality on this stock, since other sources such as general diseases, parasitism, and epizootics are not thought to be important sources of mortality on most fish stocks on an annual basis (Anderson 1979). Strong year-classes of mackerel may attract elevated levels of predation, in contrast with the usual assumption of constant natural mortality. Other studies have suggested that predation mortality rates should continually decline or remain constant as abundance increases (Sparre 1984). Our model results indicate that preda-

tion mortality rates on Atlantic mackerel are probably much higher than previously thought.

The results of the model projections show that unless the impacts of compensatory mechanisms are accounted for, evaluations of current stock status using the current standard assessment methodology may, in fact, be optimistic and risky if catches are increased to high levels in the future (Fig. 11). The differences in results between the two models are, of course, contingent on the parameterizations of the growth and predation mortality submodels and how recruitment is scaled in the density-dependent model. Two advances in research on mackerel would help to improve our ability to assess the stock: An MSVPA to provide correctly scaled estimates of recruitment, and a general predation mortality model that would provide useful estimates of M2's for forecasting purposes. Although recent assessment advice indicates that catches can be increased on the mackerel stock (Overholtz and Parry 1985), it perhaps needs to be modified to accommodate the results of this study.

The current management regime relies on catch and stock size projections based on an $F_{0.1}$ strategy. The use of a reference point such as $F_{0.1}$ is probably not very useful for mackerel since growth, sexual maturity, and natural mortality rates appear to fluctuate considerably. This concept is best applied in situations where these important variables are stable in the long term. A more appropriate approach might be to remove a moderately large sustainable catch annually or apply an appropriate constant effort level over several years, preserve a reasonable amount of spawning-stock biomass, and monitor the results. This method would be keyed to some of the uncertainties in stock dynamics that we have investigated in this study and would provide information on stock responses with a low probability of stock collapse (i.e., F = 0.2–0.3; Fig. 11C).

Additional analyses are necessary to confirm the population processes that were modeled in this study. Weights of individual fish should be monitored closely to assess future changes. Sexual maturities of ages 2–3 fish should also be followed annually. Collection of these data would also allow better parameterization of the growth and maturity models. Sufficient samples must be collected at the correct times to assess whether these two variables, particularly percent maturity, are continuing to change with stock density. Additional food habits sampling at critical times and places would help confirm and quantify the relationships found in this analysis. Obtaining some information on predation mortality on age-0 mackerel would be valuable.

Preliminary data suggest that predator preference may play an important role in determining the levels of predation on available prey species. Recent declines in sand lance *Ammodytes dubius* populations may increase predation mortality on mackerel and Atlantic herring *Clupea harengus*. This points to the need for a multispecies VPA where simultaneous impacts of predation may be investigated. Improved predation models that account for predator preference and prey abundance would allow for more accurate predictions of the impacts of these important factors, and better management advice could be provided (Livingston 1986). Larger mackerel are preyed upon by marine mammals, large pelagic fishes, and sea birds (Stillwell and Kohler 1982, 1985; Payne and Selzer 1983; Payne et al. 1984; Overholtz et al. 1990). The impact of these predators is no doubt important, but was not evaluated in this study.

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We thank the personnel from the Northeast Fisheries Center and other institutions who have collected data on research surveys over the last 25 years. We are grateful to the foreign fishery observers and scientists who collected data from the Polish commercial fishery. Special thanks to Louise Dery who provided the age data for the study. We would also like to thank Brian Rothschild for his guidance and insight in the initial phases of this research.

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Abstract.– The equilibrium contribution of hatchery-released juveniles to a rockfish fishery is evaluated by using a yield-per-recruit model. Hatchery-released juveniles may be worth up to an estimated US$0.16 per juvenile to the fishery. The use of hatchery releases to restore a depleted population of Pacific ocean perch *Sebastes alutus* is examined with the Deriso-Schnute model. This model indicates that hatchery releases have the potential to substantially increase a stock's yield and rate of recovery during the recovery period.

Evaluation of Hatchery Releases of Juveniles to Enhance Rockfish Stocks, with Application to Pacific Ocean Perch *Sebastes alutus**

Jeffrey J. Polovina

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole Street, Honolulu, Hawaii 96822-2396

There is a long history of attempts worldwide to enhance marine fisheries by releasing hatchery-reared juveniles. However, few attempts have had long-term success (Yatsuyanagi 1982, Botsford and Hobbs 1984, Isibasi 1984, Ulltang 1984). In theory, hatchery releases can enhance fisheries in two ways. First, juvenile releases can be added to the natural stock on a long-term basis to support a higher level of fishery harvest than that achieved from the natural stock alone. Secondly, juvenile releases can be used on a short-term basis to increase a depleted natural stock more rapidly, then discontinued once the natural stock has recovered.

Pilot releases of the rockfish *Sebastes schlegeli* indicate that large-scale rearing and releases of rockfish may be biologically and technically possible (Sakai et al. 1985, Kusakari In press). The merit of hatchery releases of juveniles for fishery enhancement is examined in the present paper with mathematical models. Specifically, the Beverton and Holt (1966) yield-per-recruit model will be used to evaluate the sustainable increase in fishery catches from a long-term release of hatchery-reared juveniles. The Deriso-Schnute delay-difference age-structure model (Zheng and Walters 1988) will be used to evaluate the fishery benefits from short-term juvenile releases to increase the recovery of depleted rockfish stocks.

Models and methods

To evaluate the equilibrium contribution of hatchery-released juveniles to a rockfish fishery, the Beverton and Holt (1966) equation was used to express the equilibrium yield-per-recruit as a function of the following ratios: instantaneous natural mortality to von Bertalanffy growth (M/K), length at recruitment to asymptotic length, and fishing mortality to natural mortality (F/M) (Beverton and Holt 1966). If a recruit in the yield-per-recruit model is taken to represent a hatchery-released juvenile rather than a recruit from the natural population, then the equilibrium yield per hatchery-released juvenile can be computed from yield-per-recruit tables (Beverton and Holt 1966). Specifically, let Y/R_0 denote the yield per recruit where the recruits are of some reference age, say the age at which they have just become demersal. Then the yield per released fish at age t is just

$$\frac{Y}{R_0} e^{Mt}$$

where M is the natural mortality rate from the reference age 0 until release age t. The values of Y/R_0 are tabled as a function of M/K and F/M (Beverton and Holt 1966). The equilibrium yield per hatchery-released juvenile

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Table 1

Von Bertalanffy growth (K), natural mortality (M), M/K, and maximum age for seven commercially important species of rockfish (parameter estimates taken from Pacific Fishery Management Council 1989).

Common name	M/yr	K/yr	M/K	Max. age (yr)
Pacific ocean perch	0.05	0.09	0.56	70+
Yellowtail	0.07	0.16	0.44	64
Shortbelly	0.25	0.21	1.19	12
Widow	0.15–0.20	0.15	1.17*	58
Canary	0.01–0.09	0.16	0.31*	75
Chilipepper	0.20	0.18	1.11	16
Bocaccio	0.25	0.11	2.27	36

*M taken as the midpoint of the range.

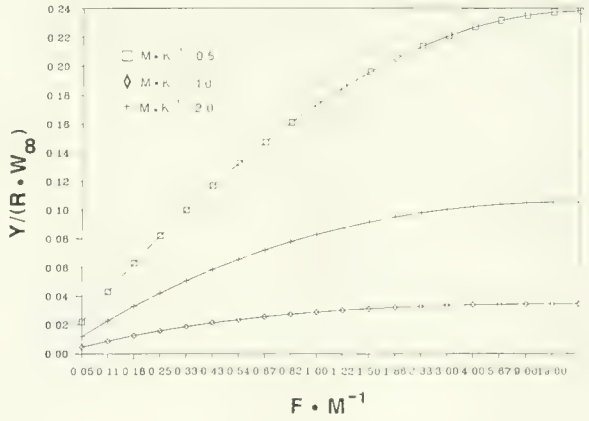

Figure 1

Beverton and Holt yield-per-recruit as a fraction of asymptotic weight at optimum size at entry to the fishery as a function of F/M for three levels of M/K.

will be estimated for values of release age t, M, M/K, and F/M, which are representative estimates for rockfish populations.

To evaluate the short-term releases of hatchery-reared juveniles to restore a depleted rockfish population, a Deriso-Schnute delay-difference age-structure model is used (Zheng and Walters 1988). Deriso (1980) derived a population model that combined simple surplus production models with more detailed age-structure models. Schnute (1985) modified this model with a three-parameter Brody growth model. This Deriso-Schnute model depends on a Brody growth parameter (p), the age of recruitment to a fishery (k), body weights at ages k and k – 1 (W_k and W_{k-1}, respectively), and total annual survival in year t (s_t). Thus, the biomass in year t + 1 ($B_t + 1$) is described as

$$B_{t+1} = (1 + p)s_t B_t - ps_t s_{t-1} B_{t-1} + R_{t+1} - ps_t \frac{W_{k-1}}{W_k} R_t,$$

where R_t is the recruitment to the fishery in year t (Schnute 1985). A Ricker stock-recruitment relationship is used to model the recruitment (in weight) from the natural rockfish population and from hatchery-released 1-year-old juveniles to the fishery to obtain the total recruitment (in weight) function (R_t):

$$R_t = AS_{t-k}\exp(-BS_{t-k})\exp(z) + H_{t-k+1}W_k\exp(-M(k-1));$$

where S_t is the spawning biomass, H_t is the number of hatchery-released 1-year-old juveniles, M is natural mortality, and A and B are constants. This model assumes hatchery juveniles are added to the natural population without any density-dependence. The term exp(z) is used to add a stochastic element to the natural recruitment function when the variable z represents a random variable, which has a normal distribution, a mean of 0, and a variance of σ^2. When σ^2 is set to 0, the stochastic term is eliminated, and deterministic recruitment is assumed. The Ricker stock-recruitment relationship appears to represent an appropriate model of recruitment in a natural rockfish population (Archibald et al. 1983).

The Deriso-Schnute model is fit to catch and fishing mortality data for Pacific ocean perch *Sebastes alutus* from Queen Charlotte Sound, Canada, during 1963–77 when the population was fished from an estimated biomass of 82,000 metric tons (t) to 13,000 t (Archibald et al. 1983). The model with its estimated parameters is then used to estimate the equilibrium yield curve to determine the biomass and fishing mortality that achieve maximum sustainable yield (MSY). Then the model with stochastic recruitment is used to simulate the recovery of this depleted stock to the biomass level that supports MSY under several management strategies, including the release of hatchery-reared juveniles.

Results

Values of M for rockfishes typically range from 0.01 to 0.25 per year, K from 0.09 to 0.21 per year, and M/K ratios from 0.44 to 2.27 (Table 1). Values of yield-

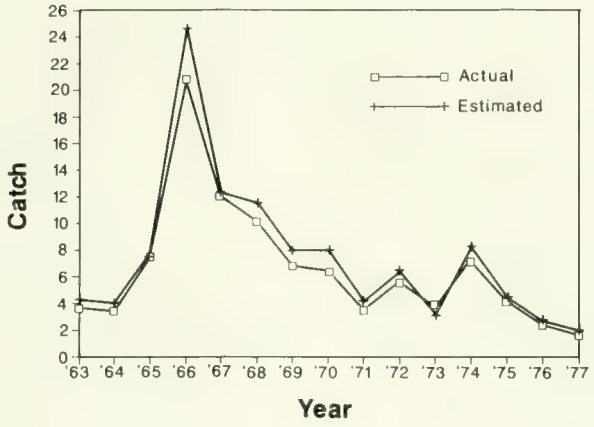

Figure 2
Historic catches (10^3 metric tons) of Pacific ocean perch from Queen Charlotte Sound and estimated catches from the fit of the Deriso-Schnute model, 1963–77.

Table 2
Parameters for the Deriso-Schnute model fit to Pacific ocean perch in Queen Charlotte Sound.

Parameter	Value	Source
Recruitment age (k)	9 years	Archibald et al. (1983)
Natural mortality (m)	0.05 per year	Archibald et al. (1983)
Weight at entry (W_k)	0.614 kg	Archibald et al. (1983)
Weight at age k – 1 (W_{k-1})	0.572 kg	Archibald et al. (1983)
Body growth (p)	0.52 per year	Estimated as mean of range: $1 - \sqrt{\frac{W_k}{W_\infty}} \leq p \leq 1 - \frac{W_k}{W_\infty}$
Recruitment model	Ricker	Archibald et al. (1983)
Recruitment parameters A, B	A = 0.29 $B = 1.6 \times 10^{-5}$	From fit of model to 1963–77 data

per-recruit (expressed as a fraction of the asymptotic weight of the fish, as a function of F/M, and for M/K equaling 0.5, 1.0, and 2.0) are shown in Figure 1. These yield curves assume that the ratio of the length-at-recruitment to the asymptotic length is optimum to achieve maximum yield-per-recruit. For M/K ranging from 0.5 to 2.0, the optimum length at harvest will be 45–86% of the asymptotic length (Beverton and Holt 1966). Thus, in the case of Pacific ocean perch, which has an asymptotic weight of about 1.4 kg, if M/K = 0.5, F/M = 1.0, and M = 0.05 per year, the contribution to the fishery of an individual juvenile released from the hatchery at age 0.25 is calculated as the product of 1.4 kg × 0.17 (from Fig. 1), multiplied by exp(0.05 · 0.25) or 0.24 kg. The average 1988 ex-vessel price for all rockfishes was US$0.67 per kg (National Marine Fisheries Service 1989); therefore, each 3-month-old, hatchery-released juvenile on the average is worth $0.16 to the fishery. The contribution of a juvenile to the fishery is strongly inversely related to M/K (Fig. 1). For example, if M/K is 1.0 rather than 0.5, then the contribution is only about one-half as much. Also, as long as natural mortality is assumed to be low and constant, changes in the release age have little influence on the contribution of the juvenile to the fishery. However, it is quite possible that natural mortality of young juveniles varies considerably by age and an optimum release age exists, although we have no data to document either case.

Pacific ocean perch in Queen Charlotte Sound, Canada, underwent heavy exploitation from 1963 to 1977 (Fig. 2) (Archibald et al. 1983). A reconstruction of the history of this exploitation by using a catch-at-age model estimates annual exploitable biomass and average fishing mortality during this period (Archibald et al. 1983). The Deriso-Schnute model is fit to the catch history of this fishery during 1963–77 by using estimates of fishing mortality from the catch-at-age model (Fig. 2). All but two of the parameters required for the model are from published values (Table 2). Two parameters (A and B in Table 2) in the stock-recruitment relationship part of the model are estimated by fitting the model to the 1963–77 catch series.

Based on the Deriso-Schnute delay-difference model with the parameters used to fit the catch and effort series (1963–77) and to estimate the equilibrium yield curve, the maximum sustainable yield (MSY) of about 1800 t is achieved at $F_{MSY} = 0.06$ per year (Fig. 3). At that level of F_{MSY}, the corresponding equilibrium biomass (B_{MSY}) is estimated at about 35,000 t. At B_{MSY}, the recruitment of 1-year-old juveniles is estimated at 3.5 million fish, whereas an estimated 1.3 million 1-year-olds recruit if biomass is at the 1977 depleted levels.

Assuming that the goal of restoring the Pacific ocean perch stock is to increase the biomass to 35,000 t so it can be harvested at F = 0.06 to achieve MSY, three approaches to stock recovery are examined. One approach has as its goal to increase the biomass to B_{MSY} as quickly as possible by setting F at 0 until the biomass reaches 35,000 t, then the stock will be fished at

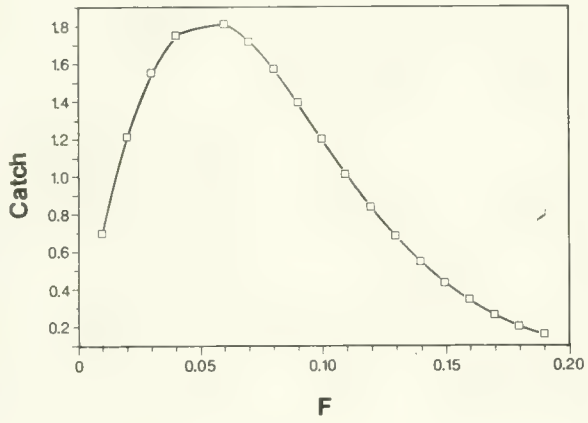

Figure 3
Equilibrium yield curve (10^3 metric tons) for Pacific ocean perch from Queen Charlotte Sound estimated from the Deriso-Schnute model.

F = 0.06. The second approach to stock recovery is to eventually achieve B_{MSY} while also maximizing the yield to the fishery. Under this approach, the stock is fished at F = 0.06 from the beginning. A third strategy, which represents a compromise between these two philosophies, will set F at 0.03 until the biomass reaches 35,000 t, then the stock will be fished at F = 0.06.

Each of these three sequences of F can be evaluated with and without hatchery releases. Catch and biomass series with and without hatchery releases for each sequence of F can be simulated with the stochastic Deriso-Schnute model with the parameters used to fit the population decline. When hatchery releases are used, 5 million 1-year-old juveniles will be stocked annually. This number represents almost four times the natural recruitment for the stock at the 1977 depleted level and about 40% more than the natural recruitment at the B_{MSY} level. The variance of the random variable z in the stochastic recruitment component is assumed to have a variance of 0.3 (Archibald et al. 1983). Based on 100 simulations of each of the six management approaches over 100 years, the mean annual catches, mean cumulative catches and the biomass distributions after 20 years can be computed (Figs. 4–6, Table 3).

When the management strategy closes the stock to fishing to restore it as quickly as possible, B_{MSY} (35,000 t) is achieved in 21 years without stocking and 14 years if 5 million juveniles are stocked annually for 6 years (Table 3). After 20 years, the mean biomass levels are about the same for the stocked and non-stocked cases, so annual catches are about the same and the difference in cumulative yield remains con-

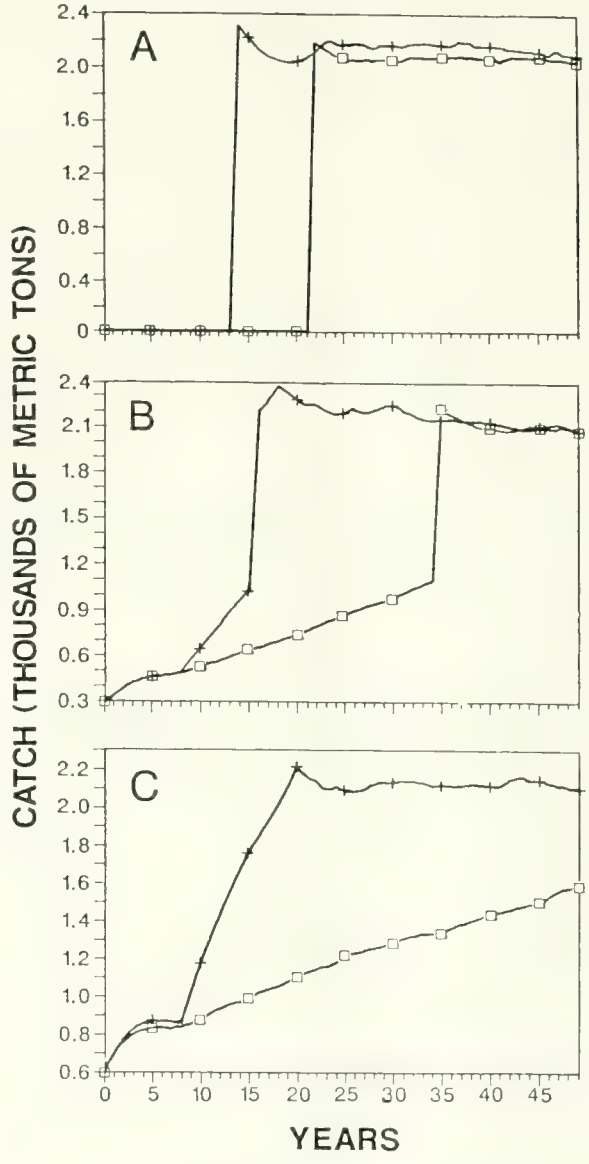

Figure 4
Simulated annual catches of Pacific ocean perch, with and without hatchery releases, for three management strategies.

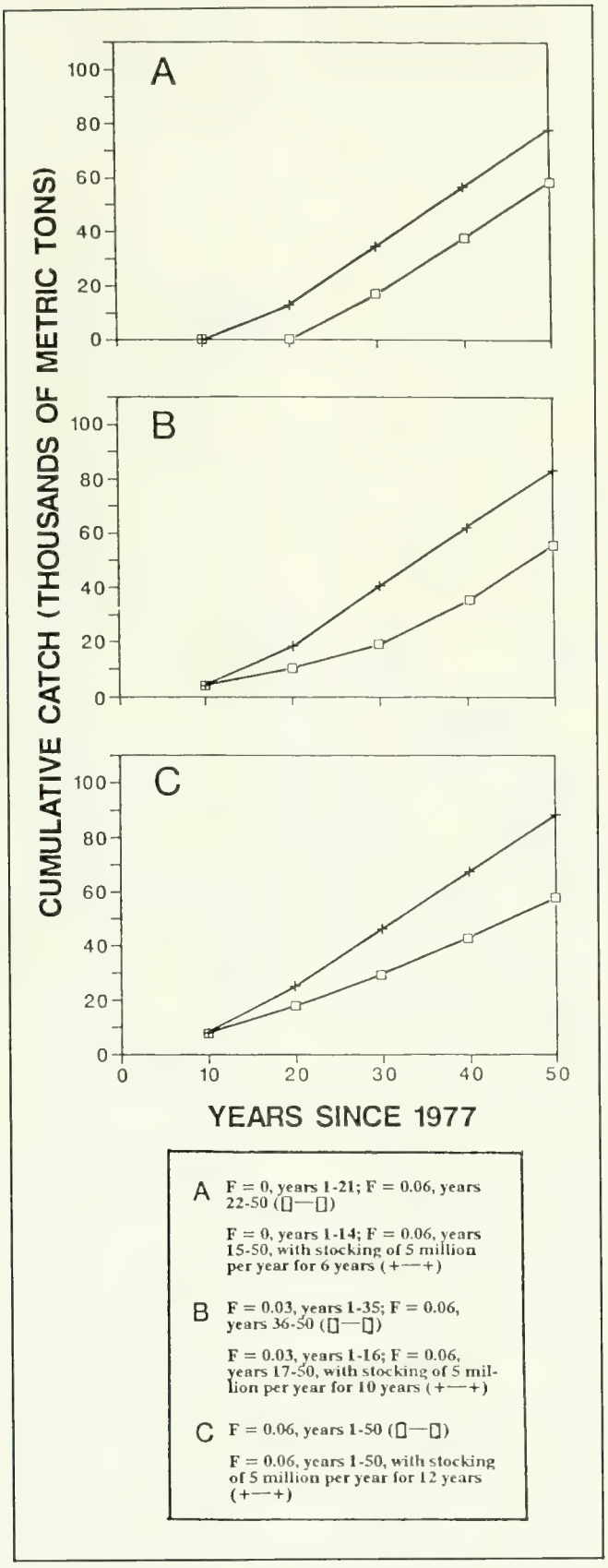

Figure 5
Simulated cumulative catches of Pacific ocean perch, with and without hatchery releases, for three management strategies.

stant (Figs. 4, 5). The biomass distributions with and without stocking are very similar after 20 years (Fig. 6).

When F = 0.03, B_{MSY} is achieved in 35 years without stocking and in 17 years when 5 million juveniles are stocked annually for 10 years (Table 3). The annual catches for both the stocked and nonstocked strategies are the same for the first 8 years because of the 8-year lag between the release of juveniles and their entry into the fishery; but beginning in year 9, the annual catches in the stocked strategy exceed those for the nonstocked strategy. In year 16, B_{MSY} is achieved in the stocked strategy, and F is increased to 0.06, which results in a substantial increase in annual catches. The annual catches for the nonstocked strategy lag behind the stocked catches until year 35 when B_{MSY} is achieved and F is increased to 0.06 (Fig. 4). The difference between the cumulative catches for stocked and nonstocked is initially very small, because the two strategies have the same annual catches at the beginning, but the difference grows once the annual catches diverge (Fig. 5). After 20 years, the distribution of biomass for the stocked population is about 10,000 t greater than for the population without stocking (Fig. 6).

When F = 0.06, B_{MSY} is not achieved within 100 years without stocking, whereas B_{MSY} is achieved in 20 years with stocking (Table 3). The patterns of annual and cumulative catches for the stocked and nonstocked cases are similar to the F = 0.03 situation (Figs. 4, 5). After 20 years, the distribution of biomass without stocking shows very little change from the level at the beginning of the recovery period, whereas the distribution of the stocked population centers close to B_{MSY} (Fig. 6).

The value of stocking to increase yields while restoring the depleted Pacific ocean perch population can be evaluated by computing the break-even cost of a hatchery-released juvenile based on the increase in cumulative landings. Suppose a hatchery, built and operated by government funds, must meet the economic criterion of a 3% return on investment. Then the break-even cost per juvenile, as a function of n years after the start of stocking, can be calculated as follows: (1) Compute the increase in cumulative yield between the comparable stocked and nonstocked strategies, n years

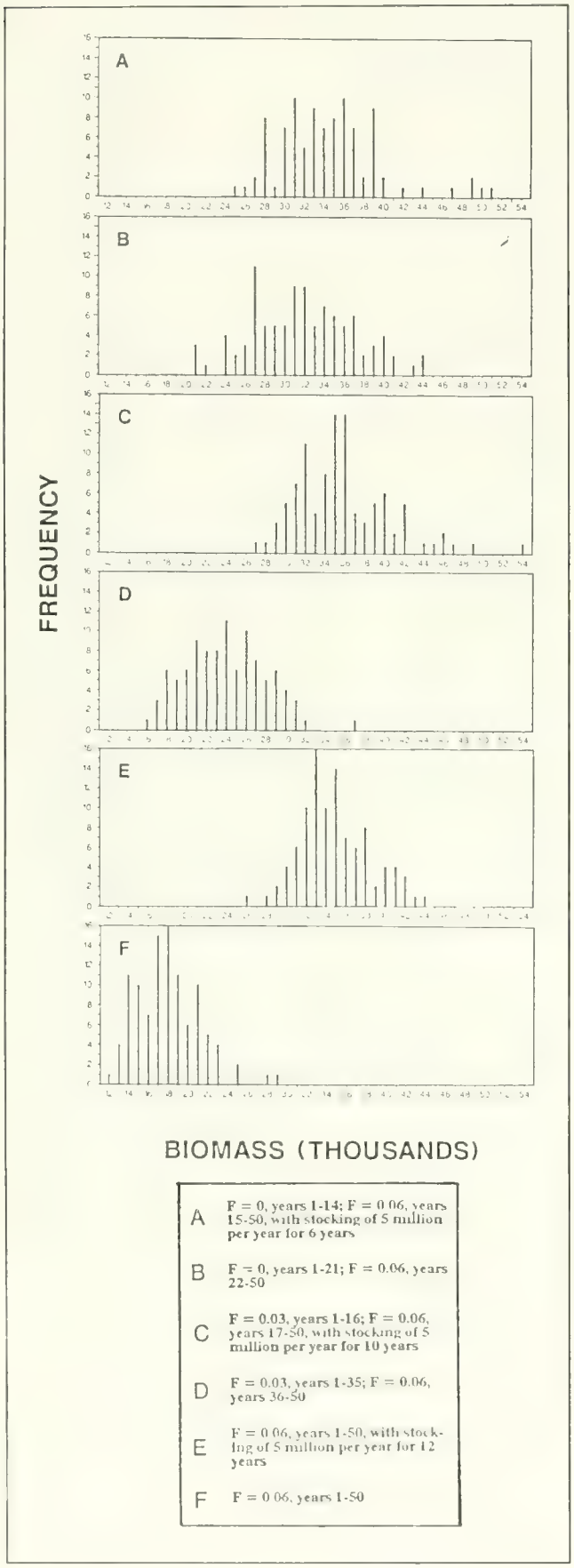

Figure 6
Biomass distributions of Pacific ocean perch 20 years after the onset of hatchery releases (from 100 simulations), with and without stocking, for three management strategies.

after the start of stocking; (2) divide this increase in yield (the result from step 1) by the total number of juveniles stocked to obtain the increase in yield per stocked juvenile; (3) multiply the result of step 2 by the unit value of the yield to the fishery to compute the value to the fishery per stocked juvenile; and, finally, (4) discount this yield cumulated over n years to a present value by dividing the result of step 3 by $(1.03)^n$. Using this approach, based on a wholesale value for Pacific ocean perch of \$0.67 per kg (National Marine Fisheries Service 1989), the break-even cost per juvenile ranges from \$0.04 to \$0.16. For example, under the scenario where the fishery is closed until B_{MSY} is reached, if hatchery juveniles can be stocked at a cost of \$0.16 per juvenile, then hatchery releases result in increasing the value of the catches over the nonstocked strategy equivalent to a 3% annual return on stocking costs for the first 20 years after stocking (Table 4). However, under the scenario where F = 0.06 from the beginning of the recovery period, the break-even cost of a hatchery-released juvenile cannot exceed \$0.04 if the release program is to achieve a 3% annual return over the first 10 years and \$0.08 over a 40-year period.

Looking at just the cumulative yields does not show all of the benefits of stocking, since some of the released juveniles contribute to an increase in standing stock. When the contribution of the released juveniles to both the fishery and standing stock is considered, the relative benefit is the same for all three stocking and harvesting strategies (Table 5).

A delay-difference model very similar to the model used in this analysis, but with a Cushing rather than Ricker recruitment function, has been fit to data on the Pacific ocean perch fishery in waters off Washington and Oregon (Ito et al. 1987). When the Cushing recruitment function is used in our model, the estimates of MSY, F_{MSY} and B_{MSY} change, but the relative contribution of hatchery releases to biomass and yield is unchanged (Table 5). Further, based on simple sensitivity analyses, the relative benefits of hatchery releases by increasing biomass and yield apparently are most sensitive to the ratio of natural mortality to growth (Table 5). Thus, as in the yield-per-recruit model, the relative benefits of hatchery releases are inversely proportional to the ratio of mortality to growth.

Table 3

Catch of Pacific ocean perch cumulated by 10-year periods from the mean of 100 simulations of the Deriso-Schnute model (thousands of metric tons).

Strategy	Years to B_{MSY} (N)	No. of years for which catch is cumulated 10	20	30	40	50
F = 0, years 1–21; F = 0.06, years 11–50	21	0	0	16.8	37.7	58.6
F = 0, years 1–14; F = 0.06, years 15–50, with stocking of 5 million/year for 6 years	14	0	13.0	34.5	56.5	77.9
F = 0.3, years 1–35; F = 0.06, years 36–50	35	4.4	10.6	19.2	35.2	56.2
F = 0.03, years 1–16; F = 0.06, years 17–50, with stocking of 5 million/year for 10 years	16	4.5	18.5	39.7	61.2	82.3
F = 0.06, years 1–50	100+	8.0	17.8	29.8	43.3	58.3
F = 0.06, years 1–50, with stocking of 5 million for 12 years	20	8.3	25.1	46.3	67.5	88.9

Table 4

Break-even cost of hatchery-released juveniles of Pacific ocean perch at a 3% annual rate of return (US$ per juvenile) as a function of years after start of releases.

Strategy	Years 10	20	30	40	50
F = 0, years 1–21; F = 0.06, years 22–50 **versus** F = 0, years 1–14; F = 0.06, years 15–20, with stocking of 5 million/year for 6 years	0	0.16	0.16	0.12	0.09
F = 0.03, years 1–35; F = 0.06, years 36–50 **versus** F = 0.03, years 1–16; F = 0.06, years 17–50, with stocking of 5 million/year for 10 years	0	0.06	0.11	0.11	0.08
F = 0.06, years 1–50 **versus** F = 0.06, years 1–50, with stocking of 5 million/year for 12 years	0	0.04	0.07	0.08	0.07

Table 5

Contribution of juvenile releases of Pacific ocean perch to biomass and cumulative yield 20 years after the start of releases.

Strategy	I Change in biomass per released juvenile (kg/fish)	II Change in yield per released juvenile (kg/fish)	II + III (kg/fish)
A	0	0.43	0.43
B	0.25	0.16	0.41
C	0.31	0.11	0.42
D	0.33	0.08	0.41
E	0.28	0.14	0.42
F	0.18	0.05	0.23
G	0.22	0.26	0.48
H	0.33	0.14	0.47

A: F = 0, years 1–21; F = 0.06, years 22–50 vs. F = 0, years 1–14; F = 0.06, years 15–50, with 5 million juvenile releases for 6 years.
B: F = 0.03, years 1–35; F = 0.06, years 36–50 vs. F = 0.03, years 17–50, with 5 million juvenile releases for 10 years.
C: F = 0.06 vs. F = 0.06, with 5 million juvenile releases for 12 years.
D: F = 0.04 vs. F = 0.04, with 5 million juvenile releases for 12 years.
E: F = 0.08 vs. F = 0.08, with 5 million juvenile releases for 12 years.
F: M = 0.1 instead of M = 0.05 and strategy C.
G: F = 0.08 vs. F = 0.08, with 5 million juvenile releases for 3 years with growth, mortality, and Cushing recruitment model (parameter estimates are from Ito et al. 1987).
H: F = 0.04 vs. F = 0.04, with 5 million juvenile releases for 5 years with growth, mortality, and Cushing recruitment model (parameter estimates are from Ito et al. 1987).

Discussion

The Beverton and Holt (1966) model provides a simple means of evaluating the equilibrium contribution of a long-term hatchery release program to the fishery. The model shows that if M/K is 0.5 for the hatchery-released juveniles from the time of release to capture in the fishery, and if the cost of each released juvenile is less than US$0.16, its value to the fishery exceeds its cost. The length-at-entry for fish in these analyses is assumed to be the length that maximizes the yield-per-recruit, that is, 45–86% of the asymptotic length. If the length-at-entry to the fishery is below this level, as with some long-lived, slow-growing fishes, the contribution of the hatchery releases to the fishery will be less than the value calculated by the model. However, the yield-per-recruit surface is relatively flat, so unless the length-at-entry is widely different from the optimum length, the reduction in the contribution of the hatchery releases should not exceed 10–15% of the

value corresponding to the optimum length-at-entry (Beverton and Holt 1966). The results of the model are particularly sensitive to levels of M/K, asymptotic weight, and market price. Interestingly, the results depend only on the ratio of M to K, and the slow growth of rockfish does not have a bearing on the equilibrium benefit of the released juveniles. Three commercially important species—Pacific ocean perch, yellowtail rockfish *Sebastes flavidus*, and canary rockfish *S. pinniger*—have M/K values around 0.5 and, from a population dynamics standpoint, offer the most potential for hatchery releases (Table 1).

Based on the Deriso-Schnute model, the level of F_{MSY} for Pacific ocean perch in Queen Charlotte Sound is estimated at 0.06 per year. This value is consistent with the finding of Archibald et al. (1983) and considerably less than the F levels of 0.2–0.5 per year during the depletion of the stock. Given the slow growth and long lag between spawning and recruitment to the fishery, stock recovery for rockfish is a long-term process. Fishery managers must decide whether the goal of the recovery program is to return the stock to B_{MSY} as quickly as possible or to follow a more gradual return while allowing fishing. Under both approaches, stocking reduces the time to reach B_{MSY} and increases the yield to the fishery. Both benefits must be considered in evaluating the merits of a hatchery-release program for stock recovery. As with the yield-per-recruit analysis, Pacific ocean perch, yellowtail rockfish, and canary rockfish are the three commercial species, based on their low M/K ratios, that offer the most potential for stock recovery with hatchery releases (Table 1).

Based on population-dynamics considerations, the use of hatchery releases for fishery enhancement appears to have merit for certain species of rockfishes. However, population dynamics represents only one part of the post-release ecology, and a fuller understanding of this ecology is necessary to predict the success of hatchery releases. For example, hatchery-reared Kuruma prawns *Penaeus japonicus* were released in a number of similar locations around Japan (Isibasi 1984). Increases in catches were documented in some instances, but no changes were evident in many others; researchers generally were unable to explain this variation (Isibasi 1984). While this analysis assumes that large-scale hatchery releases are possible, no such releases have been done, and nothing is known of the economics of a rockfish hatchery. Further, hatchery-released juveniles have been assumed to have the same behavior and natural mortality as wild stock. This may be an overly optimistic assumption because pilot hatchery releases for other species often have higher and more variable natural mortality than is thought to occur in wild stock (Kyokai 1983).

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Abstract. – We studied movement of Dungeness crab *Cancer magister* near Tofino, British Columbia using four methodologies. By the first two methods, beam trawling and trap sampling at specific locations, we inferred that males retreated to deeper water in winter and returned to shallower water in spring. Maturing females tended to move from coastal inlets to the more exposed coast. By the third method, a simultaneous analysis of crab movement and mortality using mark-recovery and fishing-effort data, we showed that dispersal was not extensive. Although insensitive to seasonal movement patterns, results of this analysis suggested a pattern of female movement consistent with that inferred from the beam trawl and trap data. By the fourth method, acoustic tagging, we learned that crab movement rates are inconsistent, having observed both large daily displacements (up to 925 m/day) and days of no discernible movement. The latter two analyses suggested that females tended to move about more than males, with the acoustic tagging results indicating less movement by both sexes during winter. Annual instantaneous total mortality, which is composed predominantly of natural mortality, for tagged sublegal-sized males was estimated at 2.5 (95% CI of 2.3–2.8). This is moderately less than our original natural mortality estimate of 2.9–4.5 and confirms that this original estimate was not grossly aberrant due to the confounding of movement with mortality. We estimated annual instantaneous total female mortality, which is also composed predominantly of natural mortality, to be considerably lower than that of males at 1.3 (95% CI of 0.8–1.8).

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Movement, Spatial Distribution, and Mortality of Male and Female Dungeness Crab *Cancer magister* near Tofino, British Columbia

Barry D. Smith
Glen S. Jamieson
Department of Fisheries and Oceans, Biological Sciences Branch
Pacific Biological Station, Nanaimo, British Columbia V9R 5K6, Canada

The Dungeness crab *Cancer magister* is fished commercially from Alaska to central California along the Pacific coast of North America. For at least four decades this highly valued species has undergone dramatic cyclical fluctuations in commercial landings, and coincidently in population abundance (Methot and Botsford 1982), along the Pacific coast from northern California to Washington. These fluctuations have had undesirable economic consequences (Botsford et al. 1983) and potentially could result in serious biological consequences (Botsford and Wickham 1978, McKelvey et al. 1980). Therefore, there has been considerable research focused on developing an understanding of this phenomenon in recent years (Botsford 1986). Studies of this intriguing problem have been pursued methodically, with competing hypotheses systematically being eliminated (Botsford 1986). However, Methot (1986) points out that our understanding of Dungeness crab population dynamics is still limited by a lack of information on basic population processes such as growth, mortality, movement, and reproduction.

Studies of basic processes serve three purposes. Firstly, new information helps us develop a more complete understanding of complex processes. Inobvious gaps in our understanding of complex processes can cause frustrating failures to explain observed phenomena. Secondly, population models will be more realistic when supported by confident parameter estimates for key rate variables of processes generally understood. Thirdly, many studies yield data and information for which there are competing explanations, and further research is required to resolve the hypotheses in competition. A relevant example is our estimate of male Dungeness crab mortality (Smith and Jamieson 1989b) for which movement from the study site was an alternate explanation for the disappearance of tagged crabs.

The primary purpose of this paper is to report some recent progress toward understanding the movement and spatial distributions of male and female Dungeness crab. Dungeness crab population dynamics were studied near Tofino, British Columbia, where a productive regional crab fishery has existed for a number of decades. This site has been a focal point for Dungeness crab studies in British Columbia since 1985 (Jamieson and Phillips 1988, Smith and Jamieson 1989a, b, c). In addition to our studies of movement and spatial distributions, we estimated male and female mortality from a simultaneous analysis of movement and mortality of tagged crabs. The experimental design addressed the problem of movement and mortality being confounded, which plagues many studies, by including information on fishing effort.

The four methodologies we employed for assessing Dungeness crab movement yielded information at different scales of resolution. Beam trawling between June 1985 and September 1986 helped us survey the gross distribution and abundance of male and female crabs 125–140 mm carapace width (CW). Trapping helped us assess the distribution and abundance of females greater than 145 mm CW. We previously assessed male abundance and exploitation using trap sampling data in Smith and Jamieson (1989b). From the beam trawl and trapping data sets we were able to infer some seasonal movement patterns, while our model for analyzing mark-recovery data enabled us to estimate proportional transfer rates of crabs among geographical zones within our study site (see Fig. 1), and mortality. Finally, by acoustic tagging and releasing male and female Dungeness crabs during two periods, August–October 1986 and November 1986–February 1987, we were able to monitor the movement tendencies of individual crabs during summer and winter. Together, all four methodologies enabled us to document a coherent description of the spatial distribution and movement patterns of male and female Dungeness crab near Tofino, British Columbia.

Figure 1

Map of the coastal region near Tofino, British Columbia, demarcating the geographical zones within the study site. Also shown are the relative net movement vectors across boundaries between adjacent zones for both male (m) and female (f) Dungeness crabs. The zone designation is indicated by the numbers both on the map and within the vector circle. These vectors illustrate the net directional tendencies across zone boundaries and their relative magnitude under the assumption of equal crab densities in all zones. An asterisk (*) indicates the vector magnitude is significantly ($P < 0.05$) different from zero. Zones 1–3 are in Lemmens Inlet; zone 5 is Browning Passage.

Methods

Site description

All beam trawling, trapping, and tagging were conducted within sheltered coastal waters near Tofino, British Columbia. These waters are generally ≈5–15 m depth and well mixed, with an annual seawater temperature range of ≈6–12°C. Substrate varies from sand along the exposed coast to mud near the head of Lemmens Inlet. These coastal waters have sustained a productive Dungeness crab fishery for several decades possibly due to local mudflats providing good substrate for juvenile crab (Armstrong and Gunderson 1985).

The study site is within Canadian Department of Fisheries and Oceans Statistical Area 24. The fishery in Statistical Area 24 accounted for 13 and 20% of the total weight of Dungeness crab landed in British Columbia in 1985 and 1986, respectively. During 1985 and 1986, 27 and 59 vessels, respectively, reported landings from Statistical Area 24. Of the 59 vessels which landed crab in 1986, 30 fished in the study site, and these 30 vessels accounted for approximately 80% of the 265 t landed from Statistical Area 24 in 1986. The fishery near Tofino was exploited year-round and fishing effort was sufficient to capture most males soon after their molt to legal size. Annual instantaneous fishing mortality was estimated at $F = 5.1–6.9$ (Smith and Jamieson 1989b). No crab fishing occurs in marine waters inland of the study site due to poor crab habitat.

Beam trawl sampling

In order to assess crab spatial distribution and abundance throughout the study site, we made more than 50 tows with a beam trawl (Gunderson et al. 1985, Gunderson and Ellis 1986) from June until August 1985. In addition, in areas where crabs were abundant and in a few other strategic areas, we made tows at approximately monthly intervals until September 1986. Date, tow depth, bottom type, and area swept were recorded for each tow. Crabs were sexed and their carapace widths measured. We define carapace width (CW) as the distance between the notches just anterior to the tenth anterolateral spines rounded down to the nearest millimeter. Area swept was estimated by multiplying the effective swept width of the beam trawl (2.3 m) by the distance towed. By ranging landmarks at the beginning and end of a tow of 5–10 minutes duration, we were able to calculate distance towed from high-resolution aerial photographs. Most tows were 200–500 m. Our beam trawl was assumed to be efficient and equally selective for crabs up to 135–140 mm CW. We captured very few crabs larger than 140 mm CW by beam trawl. Because it is unlikely a beam trawl captures all crabs in its path, minimum estimates of crab

densities were obtained by dividing the number of crabs captured in a tow by the area swept.

Trap sampling

The abundance of large (>145 mm CW) female crabs was assessed by sampling the catch of commercial fishermen onboard their vessels. The number and carapace width of crabs caught were recorded as were the date and location of the sample. We report two indices of female abundance: n/trap · soak day and virtual catch rate (Smith and Jamieson 1989a). Virtual catch rate (n/trap · day) is the rate at which crabs would enter a trap if initial entry rates were not reduced by changes in bait effectiveness over time and agonistic interactions among crabs.

Fishing effort survey

The number of traps fished by all local fishermen, including the three fishermen who agreed to maintain records of all tagged crabs recovered in the study site, was determined by interviewing fishermen at least monthly from April 1985 until November 1986. The number of traps hauled each month in each of the seven zones demarcated in Figure 1 was estimated by incorporating trap-count data with haul-frequency data. We also maintained a record of the number of our own research trap hauls. We validated our fishing effort survey by comparing the estimated number of traps in Lemmens Inlet each month, as obtained in fishermen interviews, with the number of trap buoys we counted in Lemmens Inlet each month. With few exceptions each trap buoy indicated one trap. Trap buoys were easily counted from a moving boat on calm water in this enclosed body of water. Figure 2a compares the estimated number of traps fished in Lemmens Inlet by each method and indicates that the fishermen's interviews provided an acceptable census of trap abundance.

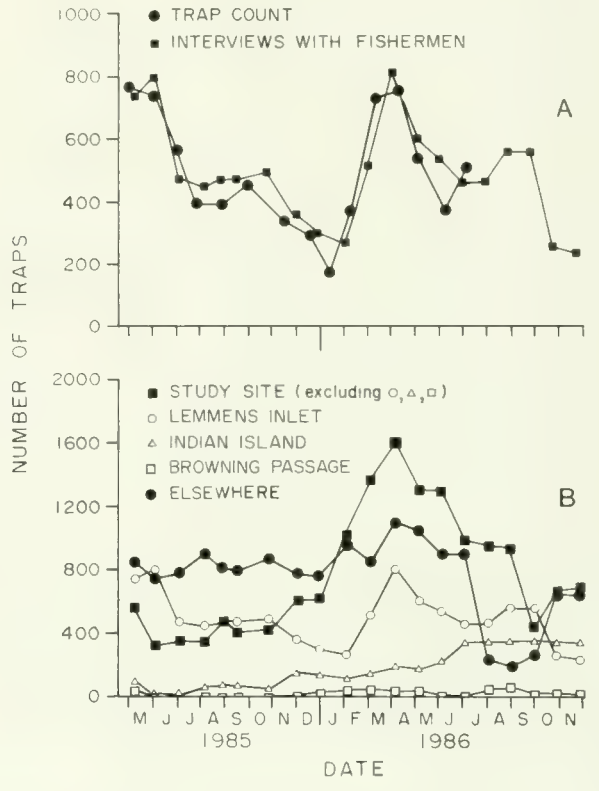

Figure 2

(A) Time-series comparison of the number of trap buoys counted in Lemmens Inlet and the number of traps estimated to be in Lemmens Inlet (zones 1–3) from interviews with fishermen. (B) Time-series of the number of traps estimated to be fishing in different regions within the study site from interviews with fishermen. 'Elsewhere' refers to traps fished outside the study site (zone 7) by fishermen who also fish within the study site.

Mark-recovery

We tagged and released 4038 sublegal-sized male ($\bar{x}$ 142 mm CW, with 95% between 106 and 162 mm CW) and 1246 female ($\bar{x}$ 150 mm CW, with 95% between 135 and 160 mm CW) Dungeness crabs from April 1985 to May 1986. Blue, individually numbered, 4.1-cm T-bar anchor tags (Floy Tag and Manufacturing Company, Seattle, WA) were inserted through the right posterior epimeral suture line, taking care not to puncture internal organs. Crabs to be tagged were obtained from research traps, fishermen, or beam trawls. Before being released, the date, location and tag number were recorded, the crabs were sexed, and their carapace width measured. Release and recovery locations were determined with a grid identification system (0.9 × 1.2 km) and landmarks.

Most recoveries were obtained from fishermen and research traps. Three fishermen recorded the date, location, and tag number of all tagged crabs they recovered on special recovery forms. Females and sublegal-sized males were returned to the water, but legal-sized males (i.e., >154 mm CW) were generally retained. We asked other fishermen to ignore the recoveries of sublegal-sized crabs, i.e., return them to the water, but to retain tags from legal-sized males. Tags were either given to us or our associates, or we had permission to board a fisherman's vessel at the dock and retrieve tags set aside. From April until August of 1985 and 1986 we saw most fishermen at least biweekly, at other times monthly.

Table 1

Zone area (km^2), fishing effort (trap hauls/month), fishing intensity (trap hauls/month · km^2), and number of tagged male and female Dungeness crabs released for geographical zones 1–7 (Fig. 1).

Zone	Area	Fishing effort	Fishing intensity	No. of tagged crabs released	
				Male	Female
1	1.23	2234	1734	1438	160
2	0.98	8655	8823	1685	286
3	0.40	16165	40718	537	76
4	0.68	9606	14106	101	95
5	1.31	1053	801	84	11
6	7.56	25294	3345	193	618
7	10^6	15736	0.0157	0	0

Analysis of movement and mortality

We simultaneously analyzed crab movement and mortality using a model structure that facilitated estimation of monthly proportional transfer rates of crabs among the seven geographical zones demarcated in Figure 1. Zone 7 essentially represents the universe outside the study site and provides the option for crabs to vacate the study site. Maximum-likelihood parameter estimates for the transfer rates and mortality were obtained by minimizing the discrepancy between observed and expected number of recoveries in each zone during consecutive one-month intervals of time-at-large. Estimation of expected numbers of recoveries required our fishing-effort survey data. This model structure allowed us to search for persistent directional movement patterns and obtain male and female mortality estimates that were not confounded by movement of tagged crabs from the study site or into a zone where fishing effort was low.

We organized 920 male and 103 female tag recoveries by the three fishermen and ourselves who recorded all tag-recovery information, and whose fishing effort over time was measured, into frequency cells (O_{ijk}) by zone released ($i = 1,...,7$), zone recovered ($j = 1,...,7$), and months-at-large ($k = 1,...,18$). Therefore, if the observed number of recoveries in cell $O_{4,1,2} = 5$, then 5 crabs released in zone 4 were recovered in zone 1 after 2 months (30–60 days)-at-large. We ignored absolute time, so our analysis was not sensitive to seasonal movement patterns. We also assumed an equal number of trap hauls each month. Although the total number of trap hauls peaks in summer due to an increase in the number of part-time fishermen (Fig. 2b), our assumption is reasonable for the three full-time fishermen, and ourselves, whose tag-recovery and trap-haul data are the only trap-haul data incorporated into this analysis. Monthly fishing intensity (Ricker 1975) for each zone was calculated by dividing the number of trap hauls each month by the area (km^2) of the zone (Table 1). Zone 7 was deliberately defined to represent an extremely large area (1 million km^2) to ensure that we did not underestimate the rate of movement of tagged crabs from the study site.

The number of tagged crabs initially released in zone i that are present in zone j after k months-at-large (N_{ijk}) is described by the following series of difference Equations (1a–g).

$$N_{i1,k+1} = (N_{i1k}(1 - \Omega_{12}) + \Omega_{21}N_{i2k})s \quad (1a)$$

$$N_{i2,k+1} = (N_{i2k}(1 - \Omega_{21} - \Omega_{23}) + \Omega_{12}N_{i1k} + \Omega_{32}N_{i3k})s \quad (1b)$$

$$N_{i3,k+1} = (N_{i3k}(1 - \Omega_{32} - \Omega_{35} - \Omega_{36}) + \Omega_{23}N_{i2k} + \Omega_{53}N_{i5k} + \Omega_{63}N_{i6k})s \quad (1c)$$

$$N_{i4,k+1} = (N_{i4k}(1 - \Omega_{45}) + \Omega_{54}N_{i5k})s \quad (1d)$$

$$N_{i5,k+1} = (N_{i5k}(1 - \Omega_{53} - \Omega_{54}) + \Omega_{45}N_{i4k} + \Omega_{35}N_{i3k})s \quad (1e)$$

$$N_{i6,k+1} = (N_{i6k}(1 - \Omega_{63} - \Omega_{67}) + \Omega_{36}N_{i3k})s \quad (1f)$$

$$N_{i7,k+1} = (N_{i7k} + \Omega_{67}N_{i6k})s \quad (1g)$$

In these equations, Ω_{ij} represents the proportion of tagged crabs in zone i that move to zone j during any one-month interval. Note that when $i = j$, N_{ij0} is number of tagged crabs released in zone i (Table 1), and that Ω_{ij}'s exist only for adjacent zones (Fig. 1). The parameter Ω_{76} could not be estimated because no tagged crabs were released in zone 7. The parameter s is monthly survival rate. The annual instantaneous rate of disappearance of tagged crabs (S) is related to s by

$$S = -12\log_e[s]. \quad (2)$$

Consequent to Equations (1a–g), the expected number of recoveries of tagged crabs released in zone i and recovered in zone j after k months-at-large (E_{ijk}) is

$$E_{ijk} = N_{ijk}\, qI_j \quad (3)$$

where I_j is monthly fishing intensity (Table 1) in zone j, and q is the catchability coefficient (Ricker 1975).

We employed a multinomial negative log-likelihood function, the separation statistic

$$f_1 = \sum_{ijk} O_{ijk}\log_e[O_{ijk}/E_{ijk}], \text{ for all } O_{ijk}>0 \quad (4)$$

of Schnute and Fournier (1980), without their factor 2, to evaluate the parameter estimates. In total, the 11 Ω_{ij}'s in Equations (1a–g), q and S required estimation. The model was structured to constrain the Ω_{ij}'s to values between 0 and 1, and to assure the multinomial likelihood condition of

$$\sum_{ijk} O_{ijk} = \sum_{ijk} E_{ijk}. \quad (5)$$

Equation (4) measures the discrepancy between observed (O_{ijk}) and expected (E_{ijk}) frequencies over all frequency cells, and yields maximum-likelihood parameter estimates when f_1 is minimized. We used the SIMPLEX algorithm of Nelder and Mead (1965) as implemented by Mittertreiner and Schnute (1985) to minimize f_1, while approximate standard errors for the estimates were calculated using the numerical method supplied with Mittertreiner and Schnute (1985). This method uses the matrix of second partial derivatives of f_1 with respect to the parameters (calculated numerically) to generate the asymptotic covariance matrix (Kendall and Stuart 1979). For males we applied the analysis only to recoveries obtained after at least one full month-at-large (k>1), because tagged males were released a short time before fisherman were prepared for the mark-recovery program. Consequently our analysis of male movement and mortality is based on a sample size of 864 recoveries rather than the complete sample of 920 recoveries.

Acoustic tagging

Freshly activated acoustic tags (Smith-Root Inc., Vancouver, WA) were attached longitudinally to the carapace of recently trap-caught hard-shelled male and female Dungeness crabs using fast-drying epoxy. Care was taken to maintain each crab cool and moist while the carapace was allowed to air-dry for a short period prior to attachment of the tag. Once the epoxy set and we were confident the bond was secure (about one-half hour), each crab was placed in a bucket with fresh seawater to assess its vitality. No crabs appeared to suffer an obvious detriment from the tagging procedure, so all crabs released were anticipated to survive and transmit location information.

Once activated, each 61 × 14 mm capsule-shaped acoustic tag emits an acoustic signal characterized by a unique transmitting frequency and pulse rate. The bulk of the tag structure is a battery with a transmitting life of ≈60–90 days. With our direction-finding equipment we were able to identify a strong signal up to ≈1 km away and subsequently home-in on the location of a tag by audibly or electronically evaluating changes in signal strength. In our study site we were generally able to define the location of a tag to within ≈10–25 m of a chart reference.

During 7–13 August 1986 two male and three female crabs were tagged with acoustic tags, then released near the mouth of Lemmens Inlet (zone 3, Fig. 1). Similarly on 15 November 1986 two male and three female crabs were again tagged and released in the same area. Following the first series of releases we attempted to monitor the location of each crab at least daily, but other commitments, and occasionally being unable to locate the transmitted signal, resulted in the time between observations often exceeding one day. The same limitations applied to the second series of releases, and additionally we only attempted to monitor each crab every three days. All crabs released provided location information for 21–86 days, with the exception of a 140-mm CW male released on 15 November 1986 which was never located after its release.

Mean daily displacement rates for males and females were estimated under the assumption that movement was random from the point of release. We could not entertain a more sophisticated hypothesis with our limited data. Also because of our limited data, we report our results for males and females, and by series (August–October, November–February), with all data from individual crabs combined. Mean daily displacement is the mean expected distance between the location of a crab at the same time on two consecutive days. The maximum-likelihood estimates for mean daily displacement rates (A) were obtained by minimizing the negative log-likelihood function

$$f_2 = \sum_{i=1}^{n} \{(D_i^2/t_i A) + \log_e[t_i A^2] - \log_e[2D_i]\},$$

$$\text{for all } D_i>0 \quad (6)$$

where n is the number of observations, and D_i is the linear displacement after t_i days for crab i. When our best measurement for any D_i was zero, we assumed a minimum D_i of 1 m so that Equation (6) was defined for all data points i = 1,...,n. Our Equation (6) is the maximum-likelihood solution to Equation (3) of Skellam (1951), or Equation (11.6) of Pielou (1977), both of whom develop a mathematical framework for describing random dispersal of individuals from a release point. As for our analysis of movement and mortality, f_2 was minimized and approximate standard errors for A were determined using Mittertreiner and Schnute's (1985) SIMPLEX package.

Results

Beam-trawl and trap sampling

Beam-trawl surveys in 1985 and 1986 captured few Dungeness crabs except in the selected locations considered in the following paragraphs. In 46 beam trawl samples, 2- to 3-year-old (≈75–145 mm CW) male and female crabs (Butler 1961, Stevens and Armstrong 1984, Smith and Jamieson 1989c) were found at densities generally less than 10/hectare (ha). Where much higher densities were found, there were significant seasonal differences, and differences in the relative proportions of males and females. Sampling since 1986 in the same locations (G. Jamieson, unpubl. data) has indicated that the overall abundance of crabs in the 75–145 mm CW size range has dropped to a low level, thus we believe the pattern of spatial and temporal distribution we describe herein is based on observations of essentially one strong year-class.

In upper Lemmens Inlet the densities of male and female 2-year-olds in summer 1985 were initially low and continued to decline throughout 1985 and 1986 (Fig. 3a). This suggests this area is a poor crab habitat since this cohort was abundant elsewhere. The highest density of males was observed in middle Lemmens Inlet (Fig. 3b). During autumn 1985 and the subsequent winter, male densities steadily increased to greater than 1200/ha. Toward the mouth of Lemmens Inlet male densities generally declined (Fig. 3c, d). Because densities of 2-year-old males elsewhere were consistently low, the increase in the number of males in middle Lemmens Inlet is suspected to be due to movement away from exposed shallow water during winter.

We suspect that these males concentrated in middle Lemmens Inlet because of poor habitat further up the inlet. This high density of males eventually decreased rapidly during late spring 1986. Most males were in the normally distributed instar with a mean carapace width of 129 mm and a standard deviation of 12 mm (Smith and Jamieson 1989c), and many molted to legal size in 1986 (i.e., to the normally distributed instar with a mean carapace width of 156 mm and a standard deviation of 13 mm). Following their molt to legal size they were quickly caught in an intense fishery (Smith and Jamieson 1989b). About 25–35% of the fishing effort in the study site was concentrated in Lemmens Inlet during spring 1986 (Fig. 2b).

A high density of 2-year-old females was observed in the narrow channel at the lower end of Lemmens Inlet in June 1985 (Fig. 3c). Density declined after this date, but increased during autumn in the entrance to Lemmens Inlet (Fig. 3d) 0.5–1.0 km seaward of the narrow channel. Female density further up Lemmens

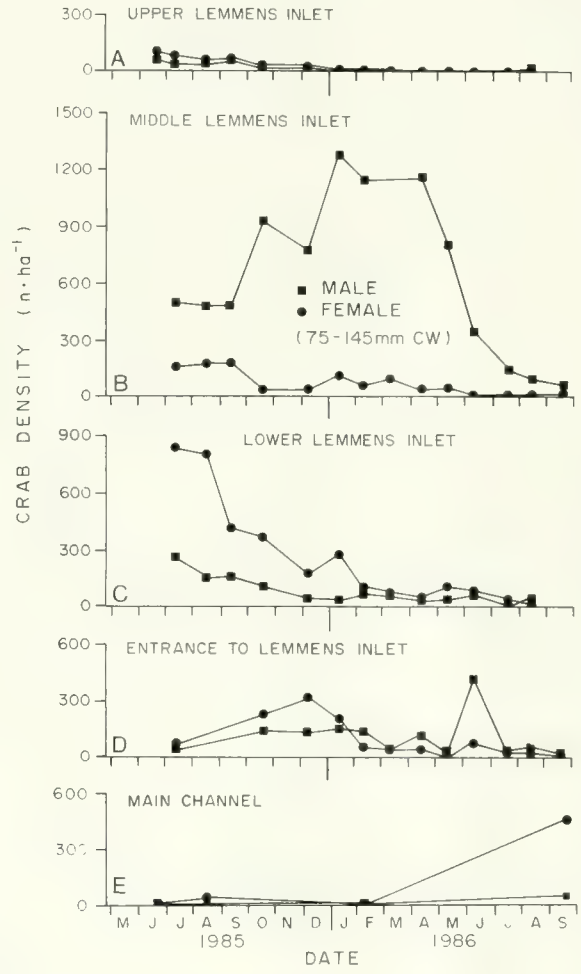

Figure 3

Time-series of densities for 2–3 year-old (≈75–145 mm CW) male and female Dungeness crabs in upper Lemmens Inlet (zone 1), middle Lemmens Inlet (zone 2), lower Lemmens Inlet (zone 2), the entrance to Lemmens Inlet (zone 3), and in the main channel out to sea (zone 6).

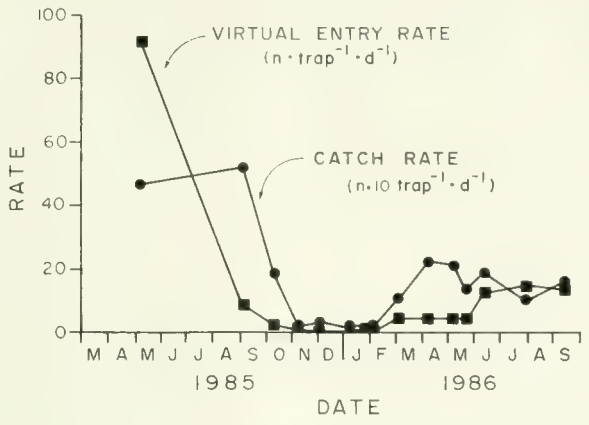

Figure 4

Two indices of abundance for female Dungeness crabs >145 mm CW in zone 6, where females were most abundant (Table 2). The virtual catch rate is the rate at which females would enter a trap if entry rates were not modified by changes in bait effectiveness over time and agonistic interactions among crabs (see Smith and Jamieson 1989a).

Table 2

Abundance (n/100 traps · soak day) of female Dungeness crabs >145 mm CW in commercial traps during May and June of 1985 and 1986.

	Female abundance	
Area samples	1985	1986
Upper Lemmens Inlet (zone 1)	7	13
Lemmens Inlet (zones 2 and 3)	15	8
Browning Passage (zone 5)	22	4
Near Indian Island (zone 4)	10	36
Main channel (zone 6)	429	138

Table 3

Maximum-likelihood estimates and standard errors (SE) of the proportion (Ω_{ij}) of tagged male and female Dungeness crabs in zone i transferring to an adjacent zone j during a one-month interval. Asterisks indicate transfer proportions significantly ($P<0.05$) greater than zero.

	Male		Female	
Parameter	Proportion	SE	Proportion	SE
Ω_{12}	0.15*	0.02	0.84*	0.25
Ω_{21}	0.50*	0.09	0.68*	0.13
Ω_{23}	0.22*	0.02	0.10*	0.03
Ω_{32}	0.16*	0.03	0.07	0.07
Ω_{35}	0.44*	0.06	0.22	0.12
Ω_{53}	0.11*	0.02	0.36	0.27
Ω_{36}	0.40*	0.04	0.63*	0.12
Ω_{63}	<0.01	<0.01	<0.01	<0.01
Ω_{45}	0.12*	0.03	0.01	0.01
Ω_{54}	<0.01*	<0.01	0.09	0.08
Ω_{67}	0.04*	0.01	0.02	0.01

Inlet continued to decline, suggesting seaward movement. The increase in female abundance in September 1986 where the main channel out of the study site meets the open coast (Fig. 3e) also suggests seaward movement of females. These females were inferred to be 3-year-olds because they were mainly in the normally distributed instar with a mean carapace width of 137 mm and a standard deviation of 9 mm (Smith and Jamieson 1989c).

The relative abundance of larger females in the study site was assessed by trap sampling. Two indices of abundance obtained from commercial trap samples (Fig. 4), show that females were most readily caught in spring, perhaps because they forage more actively after a winter of incubating eggs. The highest observed abundance of the larger females (>145 mm CW) in spring 1985 and 1986 (Table 2) was in the main channel out of the study site. This is also where (presumably) 3-year-old females in the 137 mm instar were collected in abundance by beam trawl in September 1986. This is consistent with the suggestion from beam-trawl sampling of seaward movement from local inlets as females mature.

Analysis of movement and mortality

Our estimate of the catchability coefficient q for females of 0.198×10^{-5} recoveries per trap haul was about one-seventh that for males (0.138×10^{-4} recoveries per trap haul), indicating males were much more readily caught than females by commercial traps. This difference is mainly due to commercial traps being more efficient at retaining larger crabs which are predominantly males. Consequently it is apparent in Table 3 that our transfer proportion estimates for females are much less confidently made than those for males because of the much smaller number of tagged females recovered.

The proportional transfer rates for males do not suggest any persistent directional movement. We note that there is little transfer of crabs between Indian Island (zone 4) and Browning Passage (zone 5) when compared with the apparent mixing among zones 1, 2, 3, 5, and 6, so the movement of tagged crabs through the deeper water between Browning Passage and Indian Island appears limited. Male crabs appear to vacate middle and lower Lemmens Inlet (zones 2 and 3) at proportional rates of about 0.22 and 0.40 per month with

only a small proportion per month (0.01) entering Lemmens Inlet from zone 6. The monthly proportional transfer rate of crabs from zone 2 to zone 1 (Ω_{21}) of 0.50 seems high compared with transfer of crabs from zone 1 to zone 2 (Ω_{21}) of 0.15, but this might be explained by zone 1 (upper Lemmens Inlet) being poor crab habitat and the possibility that only a small proportion of male crabs are successful in escaping this habitat.

The proportional transfer rates for females have large standard errors and must be interpreted cautiously. However, a notable result is the 0.63 proportional transfer rate for Ω_{36} compared with <0.01 for Ω_{63}, thus indicating that a greater proportion of tagged females vacated lower Lemmens Inlet than entered Lemmens Inlet. The monthly proportional transfer rate of 0.84 for females escaping the poor habitat in zone 1 (Ω_{12}) is high compared with males, but might indicate females are more capable of recognizing the environmental clues leading to more suitable substrate. The transfer rates of females in both directions between zone 1 and zone 2 are notably higher than the male transfer rates, and since the largest release of tagged male and female crabs was in zones 1 and 2, this result might indicate females are generally more mobile than males.

Proportional transfer rates alone are an incomplete interpretation of movement trends, since the zones differ in area and therefore also in crab abundance. Consequently, the high transfer rate for Ω_{36} when compared with Ω_{63} is in large part a result of zone 6 having an area of 7.56 km^2, whereas zone 3 has an area of 0.40 km^2. Relative movement vectors were therefore calculated from the transfer-rate estimates under the assumption that crab densities were equal for all zones. For example, if crab density is Δ crabs per km^2, then the estimated number of crabs transferring from zone 6 to zone 3 in a one-month period is $7.56\Delta\Omega_{63}$.

Figure 1 diagrams net movement tendencies, under the assumption of equal crab densities in all zones, across those zone boundaries where transfer rates in both directions were estimated. Two notable features for males are the strong indication of net movement of males into upper Lemmens Inlet, and a tendency for males to vacate lower Lemmens Inlet and the waters near Indian Island. As previously mentioned, the net movement into upper Lemmens Inlet might be a result of a low proportion of males escaping this poor habitat. It might also indicate dispersion from zone 2 where many males were tagged and released in spring 1986. A large number of males 125–140 mm CW were tagged in zone 2 in spring 1986 because they occurred in high density (>1200/ha) and were readily captured by beam trawl. Beam trawling indicated these crabs apparently dispersed, or molted to legal size and were caught, by summer 1986 (see previous section). For females there is a general, although non-significant, tendency to vacate Lemmens Inlet and Browning Passage. This result is consistent with our beam-trawl and trapping results (previous section) which also demonstrate a net seaward movement of females from Lemmens Inlet.

Table 4

Maximum-likelihood estimates and standard errors (SE) of mean daily displacements (A, m/d) of male and female Dungeness crabs.

	Male			Female		
	n	Estimate	SE	*n*	Estimate	SE
Aug 86–Oct 86	31	321	29	30	500	45
Nov 86–Feb 87	8	74	13	15	161	21
Combined	39	288	23	45	419	31

We estimated the annual rate of disappearance of tagged crabs with reasonable confidence at S = 2.54 (SE 0.13) and S = 1.28 (SE 0.27) for males and females, respectively. Corroborating these high estimates for S, our analysis estimated that only about 2% and 7% of tagged males and females, respectively, left zones 1–6, i.e., moved to zone 7, over the time-period of our study. In other words, the distribution over time of tag recoveries in zones 1–6 could not be well explained by a high transfer rate into zone 7 where crabs might not be recovered due to a low fishing intensity. Thus these estimates for S were obtained despite our model structure providing an exaggerated opportunity for crabs to disperse to zone 7 as an alternative explanation for the disappearance of tagged crabs, i.e., as an alternative to mortality. This conclusion appears to validate our original assumption that few tagged crabs left our study site during the study period (Smith and Jamieson 1989b).

Based on a double-tagging study, Smith and Jamieson (1989b) concluded that tag loss by sublegal-sized crabs is low and therefore unlikely to be an important source of tag disappearance. Observations of tank-held crabs over several months did not reveal differential mortality of tag and untagged crabs. Thus we conclude that the values for S estimated in this study represent mainly natural mortality and, in the case of males, tag disappearance due to molting to legal size with subsequent exploitation. However, because only about 5% of tagged sublegal-sized males were reported caught as legal-sized crabs (210 recovered when legal-sized of the 4038 released when sublegal-sized), despite high fishing mortality (F = 5.1–6.9) and apparently good compliance in reporting recovered tags (≈87%), we con-

clude that our male estimate for S measures mainly natural mortality of sublegal-sized males. We recognize, however, that there is likely some degree of mortality due to trapping and handling by fishermen. Similarly, and in consideration that females are not commercially fished, we are confident that our female estimate for S also mainly measures natural mortality.

Acoustic tagging

From the means and standard errors of the movement rate estimates (Table 4) we conclude that for both the August and November 1986 releases of acoustically tagged crabs, females tended to move about significantly ($P<0.01$) more than males. Similarly, during August–October 1986 both males and females seemed to move at rates about 3 to 4 times faster ($P<0.01$) than those for November 1986–February 1987. We realize, however, that our male results for the latter time period are based on observations of just one crab. Slower movement during winter for both male and female crab is consistent with the poikilothermic habit of marine invertebrates in that respiratory activity is closely related to temperature. Our analysis of movement based on the mark-recovery data also hints that females are more mobile than males.

We cannot conclude that our estimate of a faster movement rate for females, relative to males, represents a general phenomenon for all Dungeness crab populations. Our acoustic tagging results are possibly peculiar to our study site, since the greater movement rate for females is consistent with our interpretation of the trapping and beam trawl results which suggest that females tend to vacate the coastal inlets in search of the exposed coast. Further, we caution that our dispersal rate estimates for males and females from the acoustic tagging data should be considered minimum estimates because the archipelago in which the acoustically tagged crabs were released will tend to restrict the potential for movement. Also, our assumption of random dispersal from the point of release of an acoustically tagged crab is probably too strict. Our beam trawl and trapping data indicate that both males and females might move in response to environmental clues such as tides and currents; and our beam-trawl, trapping, and mark-recovery data all suggest seaward movement of females from Lemmens Inlet.

These limitations to our interpretation of the acoustic tagging data preclude us from obtaining precise rates of population dispersal over time. However, we think that there is some value in presenting approximate dispersal rates since they can be compared with the results of our analysis of movement and mortality, and to some degree with Dungeness crab movement rates that might be obtained from other regions. Consequently, the mean daily displacement rates (A) of 288 m/day and 419 m/day obtained for males and females, respectively, suggest that after one year of random dispersal, in the absence of geographical boundaries, 95% of males and females would be within radii of 9.5 and 13.9 km, respectively, of the point where they were one year previous. These radii were determined from

$$r^2 = -\log_e[p_{rt}]A^2t \quad (7)$$

where r is the radius within which the proportion $1 - p_{rt}$ of a randomly dispersing population is expected after t days (Pielou 1977). These estimates of r agree favorably with the results of our simultaneous analysis of movement and mortality from our mark-recovery data in that about 2% and 7% of male and female crabs, respectively, were estimated to leave the study site during the 18-month study period. The study site encompasses an area of about 5–10 km radius around Tofino (Fig. 1).

Discussion

The four methodologies we employed to assess male and female Dungeness crab movement provided insights at different levels of resolution and from different perspectives. The methodologies were complementary and together allowed us to document a coherent description of Dungeness crab movement near Tofino, British Columbia. For example, acoustic tagging gave us a general indication of the dispersal rates for individual male and female crabs (summer and winter) which was consistent with the results of our simultaneous analysis of movement and mortality using mark-recovery data. The former analysis suggested that the dispersal rates would maintain 95% of the male and female populations within about 10 km and 14 km, respectively, of points of release, while the latter analysis suggested that only about 2% of males and 7% of females would escape the study site (about 10–15 km radius) during our 18-month study period. In addition, both the beam-trawl and trap samples documented seasonal changes in the relative distributions and abundances of males and females which could not be gleaned from the acoustic tagging and mark-recovery data alone.

Overall, our four sources of movement information suggest that male Dungeness crab undergo only limited movements within the local archipelago. There was no evidence of migratory movement, but males were inferred to move to shallower water (≈10 m) during summer, then to retreat to more sheltered habitat in autumn. Others have observed, or inferred, similar behavior for this species. Stevens and Armstrong (1984)

reported that juvenile males and females of the 1980 year-class in Grays Harbor, Washington, disappeared during the winter of their first year, then reappeared the following spring. Gotshall (1978) observed movement of sublegal- and legal-sized male crabs in northern California to deeper water in winter, and a return to shallower water in spring. It is reasonable to surmise that the autumn movement to deeper water is to avoid rough shallow water during the winter. Returning to shallower, warmer, and more productive water during summer could enhance growth and survivorship.

Our estimated average daily displacement rate for male Dungeness crabs of ≈300 m/day, is consistent with our inferences on movement from our mark-recovery, beam-trawl, and trap sampling results. Our general conclusion of limited movement is also consistent with the results of other tagging studies. Both Butler (1957) for Dixon Entrance, British Columbia, and Gotshall (1978) for northern California, suggested that Dungeness crab populations remain local. With the exception of the apparent seasonal shift in habitat, no studies suggest migratory movements for males; however, Gotshall (1978) noted that males seem to move in the direction of prevailing currents off northern California. Bennett and Brown (1983) report that most tagged males of the closely related crab *Cancer pagurus* remained near where they were released in the English Channel.

Our acoustic tagging and mark-recovery data suggest that female Dungeness crab undergo only limited movement. Diamond and Hankin (1985) similarly argued that mature female Dungeness crab off the coast of northern California undergo limited movements and suggested that females constitute localized stocks. Diamond and Hankin (1985) do suspect that females move short distances to shallower water in spring to mate and molt. Our analyses provided no evidence of this, but it is quite conceivable that both males and females could improve mating opportunities by concentrating in shallow water (Butler 1960).

We inferred, mainly from our beam trawl and trap samples, that females tended to move from coastal inlets to an area more exposed to the open coast (zone 6, Fig. 1). In the inlets the substrate ranged from mud to a mud/sand mix, whereas in the more exposed area the bottom was mainly sand or a sand/gravel mix. Wild (1980) states that females must be at least partially buried in sandy substrate to extrude and incubate eggs so our inference is consistent with the current understanding of the life history of Dungeness crab females. Stevens and Armstrong (1984) noted that egg-bearing females were rare in Grays Harbor, and speculated that most mature females left the harbor to incubate and release their eggs in a preferred environment. Our study yielded an average daily displacement rate for females (≈400 m/day) which was significantly ($P<0.01$) more than the rate for males (≈300 m/day), and which might be explained by females undergoing deliberate migratory movements to locate suitable substrate for incubating eggs.

Similar movement behavior has been reported for females of other crab species. Hyland et al. (1984) observed the movement of female portunid crab *Scylla serrata* from an estuarine environment, where they lived as juveniles, to the open ocean where they released their eggs. Some females returned to inshore waters after the hatching season. Bennett and Brown (1983) demonstrated that female *C. pagurus* undergo extensive movements, apparently to locate habitat more suitable for egg incubation and release. While SCUBA diving, Howard (1982) observed egg-bearing female *C. pagurus* congregated in relatively deep (24 m), quiet water. Since they were rare elsewhere, he concluded this was a preferred habitat. Dinnel et al. (1987) observed a similar behavior for Dungeness crab in Puget Sound, Washington, from the Government of Canada submersible *Pisces IV*.

Our simultaneous analysis of Dungeness crab movement and mortality using mark-recovery and fishing-effort data diminished the confounding of these two processes and yielded a revised estimate of the natural mortality rate originally proposed by Smith and Jamieson (1989b). Our (mainly) natural mortality rate estimate for males of 2.5 (95% CI of 2.3–2.8) is moderately lower than our previous estimate of 2.9–4.5, probably because of dispersal of tagged crabs into zones (especially zone 6) with low fishing intensities.

Our estimate of female natural mortality of 1.3 (95% CI of 0.8–1.8) is significantly lower than that of males but in general agreement with the mortality estimates of Hankin et al. (1985, 1989) for females in northern California. They estimated annual instantaneous natural mortality for females greater than 140 mm CW at 2.0 and 2.5 for two different periods of release in a mark-recovery experiment. For females 125–140 mm CW their rough estimate was ≈0.7, a more precise estimate being unobtainable due to females this size having a high probability of molting and changing vulnerability to traps. Our estimate of 1.3 is based on a group of tagged females whose carapace widths at release were 135–171 mm ($\bar{x}$ 150 mm), thus our estimate seems consistent with those of Hankin et al. (1985, 1989).

The estimates of male and female natural mortality from this study, and of female natural mortality from Hankin et al. (1985, 1989), for crabs near the Canadian minimum legal size limit of 154 mm CW (165 mm spine-to-spine CW) increases our confidence that mortality of mature Dungeness crab is indeed high. For example, a mortality rate of 2.0 means only 13.5% annual

survivorship. The recognition of such a high mortality rate for adults of this commercially important species immediately prompts questions regarding the appropriateness of both the Canadian and American (≈159 mm CW) minimum legal carapace width limits for optimizing two of the most basic stock-management guidelines: yield-per-recruit and eggs-per-recruit.

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Abstract.– A logbook program was initiated to determine the relative abundance of selected fish species around oil and gas platforms off the Louisiana coast. Logbooks were maintained by 55 anglers and 10 charterboat operators from March 1987 to March 1988. A total of 36,839 fish were caught representing over 46 different species.

Principal component analysis (PCA) grouped the seventeen most abundant species into reef fish, pelagic fish, bluefish–red drum, Atlantic croaker–silver/sand seatrout, and cobia–shark–blue runner associations. Multiple regression analyses were used to compare PCA groupings to physical platform, temporal, geological, and angler characteristic variables and their interactions. Reef fish, Atlantic croaker, and silver/sand seatrout abundances were highest near large, structurally complex platforms in relatively deep water. High spotted seatrout abundances were correlated with small, unmanned oil and gas platforms in shallow water. Pelagic fish, bluefish, red drum, cobia, and shark abundances were not related to the physical parameters of the platforms.

Factors Affecting the Abundance of Selected Fishes near Oil and Gas Platforms in the Northern Gulf of Mexico*

David R. Stanley
Charles A. Wilson

Coastal Fisheries Institute, Center for Wetland Resources
Louisiana State University, Baton Rouge, Louisiana 70803

Louisiana has long been recognized as having abundant fisheries resources as evidenced by the large number of recreational and commercial fishing opportunities. This is particularly true of its offshore waters which Moore et al. (1970) characterized as having high densities of demersal fishes and Gunter (1963) postulated were the most productive waters on earth based on fishery harvests.

Saltwater sportfishing off Louisiana is concentrated around oil and gas platforms with an estimated 37% of all saltwater angling trips (Witzig 1986) and over 70% of all recreational angling trips in the Exclusive Economic Zone (more than 3 miles from shore) occurring around platforms (Reggio 1987). All of the 3700 oil and gas platforms off the coast of Louisiana are thought to act as artificial reefs and have contributed to Louisiana's designation as a fishing "paradise."

Gallaway (1984) estimated that oil and gas platforms constitute 28% of the known hard substrate off Louisiana and Texas. This is of particular importance off the Louisiana coast since the nearest natural hard bottom habitat is approximately 92 km from shore (Sonnier et al. 1976); therefore, oil and gas platforms provide the only source of hard-bottom habitat close to shore. The continued growth of the offshore oil and gas industry in Louisiana has provided habitat expansion for organisms dependent on hard substrate (Sonnier et al. 1976, Gallaway et al. 1981a, Continental Shelf Associates 1982).

Oil and gas platforms are unique as artificial reefs because they extend throughout the entire water column. Their effects are not confined to benthic and demersal fishes; pelagic fishes also benefit (Gallaway et al. 1981a, Continental Shelf Associates 1982). For example, pelagic baitfish (i.e., round scad *Decaptarus punctatus*, Spanish sardine *Sardinella anchovia*, and scaled sardine *Harengula pensacolae*) often maintain a position from nearsurface to mid-depth within or upcurrent from oil and gas structures feeding on plankton and zooplankton, while large predatory pelagic fishes (i.e., king mackerel and blue runner) are reported to swim from the surface to mid-depth around structures, rarely venturing within the structure (Hastings et al. 1976, Gallaway et al. 1981a).

Although oil and gas structures, like most artificial reefs, are considered to increase production and attract fish, there are few accepted techniques to assess their effectiveness. A method of testing the success or importance of an artificial reef is to track the number of fish caught over time. Due to the complex construction of oil and gas platforms, sampling with traditional fisheries

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gear (e.g., trawls, gillnets) is difficult at best; therefore, the number of fish caught per angler/hour (CPUE) was used to estimate the relative abundance of fish near oil and gas platforms.

Artificial reefs have been reported to concentrate scattered fishes and/or elevate secondary production by increasing the growth and survival of new individuals. However, few studies have examined the trophodynamics of these systems (Bohnsack and Sutherland 1985). The attraction/production paradigm should not be viewed as a black and white issue, but as a gradient depending upon species, life-history stage, type of artificial reef, etc. (Bohnsack 1989). Many species of fish around oil and gas platforms are trophically independent of the structure (e.g., pelagic fishes), but may use the platform for other purposes (e.g., optical stimulus, shelter, protection from predation, seasonal movements, spawning and orientation) (Gooding and Magnuson 1967, Hunter and Mitchell 1967, Klima and Wickham 1971, Wickham et al. 1973, Gallaway et al. 1981a, Continental Shelf Associates 1982).

Factors that may explain the congregation of fish around artificial reefs are poorly known (Grove and Sonu 1983). Some theories on factors influencing the abundance and attraction of fish to artificial reefs include shape and complexity (Hunter and Mitchell 1968, Luckhurst and Luckhurst 1978, Grove and Sonu 1983, Chandler et al. 1985), size of the artificial reef (Hunter and Mitchell 1968, Huntsman 1981, Grove and Sonu 1983, Turner et al. 1969, Rousenfell 1972, Ogawa 1982, Vik 1982), age of the artificial reef and seasonality (Turner et al. 1969, Molles 1978, Stone et al. 1979, Smith 1979, Lukens 1981, Stephens and Zerba 1981). Colonization of natural and artificial reefs did not follow the MacArthur and Wilson (1967) model of species equilibrium for insular biotas according to Smith (1979) and Lukens (1981). They found the strong seasonal effects in the northern Gulf of Mexico produced seasonally stable communities with regular fluctuations in diversity and abundance.

The objective of this study was to determine if a relationship exists between the relative abundance of selected fish species near oil and gas platforms off the Louisiana coast and (1) physical platform variables (e.g., water depth, submerged surface area, volume of water enclosed by the platform, mode of platform operation, platform age), (2) temporal variables (e.g., linear, quadratic, and cubic functions of date), (3) meteorological and geological variables (e.g., air temperature, wind speed and direction, mean sediment size), and (4) angler characteristic variables (e.g., fishing method, boat length, total engine horsepower, presence of electronic fishing aids).

Materials and methods

Between September 1986 and March 1987 we solicited 120 recreational anglers from fishing clubs across Louisiana to maintain logbooks. In addition, 23 of the charterboat operators listed in National Marine Fisheries Service records and Coleman (1984) volunteered to maintain logbooks. Logbook data were collected from March 1987 to March 1988. The design of the logbook and data collected were based on the Lake Erie Angler Diary Program (Sztramko 1986) and logbook criteria outlined by Demory and Golden (1983). Information obtained from the logbooks included: date of trip, number of anglers, oil and gas platform fished, fishing time (not including travel time), fishing method, bait used, and the species and number of fish caught. Due to the difficulty in identification of some fish species, snapper other than red snapper, groupers, sharks, and silver and sand seatrout were classified as other snapper, groupers, sharks, and silver/sand seatrout respectively. Other data acquired from logbook participants included boat length (m), total engine horsepower, and the presence of electronic fishing aids (e.g., LORAN, graph recorders, and echosounders) which assisted in the capture of fish.

We also measured characteristics of the platform, surrounding sediments, and weather which we considered important. Submerged surface area (m^2), volume of water enclosed by the structure (m^3), and the number of legs, wells, and structural crossmembers for each platform utilized by the logbook participants were calculated from drawings and information provided by offshore oil operators. Water depth (m) and age of the structures were supplied by the Minerals Management Service. Surface sediment sizes (μm) adjacent to oil and gas structures were taken from Coleman et al. (1986). Meteorological data, including average daily wind speed (km/hour), direction, and temperature (°C), for the New Orleans International Airport were obtained from the Louisiana State Climatology Office.

To account for seasonal differences in abundance, linear, quadratic, and cubic orthogonal polynomials of the 12 months of the study were used. Orthogonal polynomial contrasts are by definition uncorrelated, thus enabling the unique contribution of the linear, quadratic, or cubic effects of time to be identified.

CPUE was calculated as the number of fish caught per angler per hour of fishing. Prior to any analysis that assumes data normality, the distribution of CPUE data was tested and found not to be normal. Therefore, in order to approximate the normal distribution, the CPUE data were transformed by $\ln(\text{CPUE} + 1)$ due to the large number of zero values in the original data (Pennington 1983, 1985).

Two multivariate analysis techniques were utilized to determine the relationships between species abundance and geological, physical, temporal, and meteorological variables. Principal Component Analysis (PCA) was used on the individual fish species as a data-reduction technique. The PCA transforms the original set of variables into a smaller set of orthogonal linear combinations of species that account for a major portion of the variance in the original set (Chatfield and Collins 1980, Dillon and Goldstein 1984). The CPUE data from 17 species or species groups were reduced to 5 principal components (PC's) using the FACTOR procedure (SAS 1985). Only PC loadings greater than 0.35 were considered; although the value of 0.35 is arbitrary, it implies at least 12% of the variance of the species variable was accounted for by the PC. The component scores of the five PC's were used in subsequent multiple-regression analyses.

Stepwise multiple-regression analyses (MRA) were performed with spotted seatrout ln(CPUE + 1) and the component scores of each PC on the angler characteristics, meteorological, temporal, geological, and physical platform data and their interactions (predictor variables) (Table 1). An MRA of the predictor variables and ln(CPUE + 1) of spotted seatrout was treated as a separate analysis because spotted seatrout represented 24.8% and 28.3% of the total number of fish caught by anglers and charterboat operators, respectively (Table 2), and because they did not load positively with the other species in the PCA. The MRA was executed using the STEPWISE procedure with the MAXR option in SAS (1985). Unless otherwise stated, all differences discussed are significant at the $\alpha = 0.01$ level of significance.

Table 1

Temporal, meteorological, angler characteristic, physical platform, and geological variables and their interactions used in the multiple regression analysis.

Angler	**Physical**
Fishing method	Structure age
Boat length	Number of crossmembers
Engine horsepower	Number of legs
Presence of echosounder	Number of wells
Presence of LORAN	Water depth
Presence of graph recorder	Submerged surface area
	Volume of water enclosed
Geological	Structure manned
Mean sediment size	Structure in production
	Temporal/meteorological
	Linear date
	Quadratic date
	Cubic date
	Wind speed
Interactions	Wind direction
Boat length × Hp	Air temperature
Quadratic structure age	
Structure age × number of legs	
Structure age × number of crossmembers	
Structure age × submerged surface area	
Number of legs × number of cross members	
Number of legs × number of wells	
Number of legs × enclosed volume	
Number of legs × submerged surface area	
Structure manned × structure in production	
Water depth × volume of water enclosed	
Water depth × submerged surface area	
Submerged surface area × volume of water	

Results

A total of 55 anglers and 10 charterboat operators returned logbooks with usable information, a 45.8% and 43.5% return rate, respectively. The participants fished at 467 different oil and gas platforms a total of 1196 separate times. Anglers fished at platforms on 666 occasions and caught a total of 20,559 fish representing over 46 different species (Table 2). Charterboat operators fished at platforms 530 times and caught a total of 16,280 fish representing over 42 different species (Table 2).

A five-factor PCA explained 45.7% of the variance of the original data set and allowed us to reduce the data from the 17 separate species or species groups into a smaller data set of presumably related species (Table 3). The first factor was defined as a reef fish factor which included high positive loadings for greater amberjack, grey triggerfish, grouper, other snapper and red snapper, and a negative loading for spotted seatrout (Table 3). The pelagic fish factor consisted of positive loadings for dolphin, king mackerel, little tunny and Spanish mackerel, and a negative loading for silver/sand seatrout (Table 3). The third factor was composed of high positive loadings of Atlantic croaker and silver/sand seatrout (Table 3). The fourth factor was composed of high positive loadings of bluefish and red drum (Table 3). The fifth consisted of positive loadings for cobia and sharks, and a high negative loading for blue runner (Table 3). The strongest ecological relationships within a PC existed for reef fish and pelagic fish PC's. These groupings included species with similar life histories, habits, and abundances. The biological relationships between the species in the other PC's were more tenuous; however they did provide information on factors relating to the species relative abundance.

Results of the MRA of ln(CPUE + 1) of spotted seatrout with the predictor variables indicated spotted seatrout abundances were highest near small, non-producing structures in shallow water. Fourteen

Table 2

Composition of catch around oil and gas platforms of angler and charterboat operator logbook participants, March 1987–March 1988.

	Angler		Charterboat operator	
Species/Group	No. caught	Percent	No. caught	Percent
Atlantic croaker (*Micropogonias undulatus*)	385	1.9	327	2.0
Atlantic spadefish (*Chaetodipterus faber*)	16	0.1	3	0.0
Bearded brotula (*Brotula barbata*)	14	0.1	—	—
Black drum (*Pogonias cromis*)	118	0.6	8	0.0
Blackfin tuna (*Thunnus atlanticus*)	20	0.1	5	0.0
Bluefish (*Pomatomus saltatrix*)	699	3.4	460	2.8
Blue marlin (*Makaira nigricans*)	2	0.0	2	0.0
Blue runner (*Caranx fusus*)	209	1.0	70	0.4
Cobia (*Rachycentron canadum*)	216	1.1	203	1.2
Crevalle jack (*Caranx hippos*)	41	0.2	19	0.1
Cubbyu (*Equetus umbrosus*)	5	0.0	—	—
Dolphin (*Coryphaena hippurus*)	209	1.0	172	1.1
Florida pompano (*Trachinotus carolinus*)	5	0.0	324	2.0
Flounder (*Paralichthys* sp.)	1	0.0	7	0.0
Gafftopsail catfish (*Bagre marinus*)	56	0.3	17	0.1
Great barracuda (*Sphyraena barracuda*)	19	0.1	27	0.2
Greater amberjack (*Seriola dumerili*)	625	3.0	1086	6.7
Grey triggerfish (*Balistes capriscus*)	635	3.1	211	1.3
Grouper (Family: Serranidae)	422	2.1	583	3.6
Grunts (*Haemulon* sp.)	44	0.2	5	0.0
Hake (*Urophycis* sp.)	1	0.0	2	0.0
Hardhead catfish (*Arius felis*)	301	1.5	133	0.8
King mackerel (*Scomberomorus cavalla*)	198	1.0	292	1.8
Ladyfish (*Elops saurus*)	20	0.1	3	0.0
Little tunny (*Euthynnus alletteratus*)	183	0.9	147	0.9
Lookdown (*Selene vomer*)	9	0.0	—	—
Other jacks (*Caranx* sp.)	49	0.2	14	0.1
Other snapper (Family: Lutjanidae)	443	2.2	809	5.0
Pinfish (*Lagodon rhomboides*)	66	0.3	70	0.4
Puffer (Family: Tetraodontidae)	1	0.0	—	—
Rainbow runner (*Elagatis bipinnulata*)	1	0.0	—	—
Rays (Family: Dasyatidae)	1	0.0	1	0.0
Red drum (*Sciaenops ocellatus*)	622	3.0	637	3.9
Red snapper (*Lutjanus campechanus*)	7315	35.6	3977	24.4
Sharks (Order: Selachii)	165	0.8	236	1.4
Sheepshead (*Archosargus probatocephalus*)	31	0.2	4	0.0
Shrimp eel (*Ophichthus* sp.)	—	—	10	0.1
Silver/sand seatrout (*Cynoscion* sp.)	1716	8.3	1407	8.6
Skipjack tuna (*Euthynnus pelamis*)	3	0.0	157	1.0
Spanish mackerel (*Scomberomorus maculatus*)	484	2.4	211	1.3
Spotted seatrout (*Cynoscion nebulosus*)	5108	24.8	4605	28.3
Squirrelfish (*Holocentrus* sp.)	—	—	12	0.1
Tarpon (*Megalops atlanticus*)	3	0.0	1	0.0
Tripletail (*Lobotes surinamensis*)	65	0.3	7	0.0
Wahoo (*Acanthocybium solanderi*)	19	0.1	10	0.1
White spotted soapfish (*Rypticus maculatus*)	9	0.0	—	—
Yellowfin tuna (*Thunnus albacares*)	5	0.0	—	—
Total	20,559		16,280	

significant predictor variables explained 42.2% of the variance contained in spotted seatrout ln(CPUE + 1) (Table 4). Water depth had the highest partial correlation coefficient (r^2) and a negative regression coefficient (Table 4), indicating that spotted seatrout were more prevalent in shallow water. Regression coefficients were negative for submerged surface area × volume of water enclosed, submerged surface area,

Table 3

Common factor analysis using principal component analysis for the first five factors of ln(CPUE + 1) for the 17 most frequently caught species by logbook participants, March 1987–March 1988. Loadings below 0.35 are marked with a dash.

	Principal component				
Species/Group	Reef fish	Pelagic fish	Atlantic croaker Silver/sand seatrout	Bluefish Red drum	Cobia Bluerunner Shark
Atlantic croaker	–	–	0.755	–	–
Bluefish	–	–	–	0.766	–
Bluerunner	–	–	–	–	−0.681
Cobia	–	–	–	–	0.379
Dolphin	–	0.406	–	–	–
Greater amberjack	0.664	–	–	–	–
Grey triggerfish	0.515	–	–	–	–
Grouper	0.691	–	–	–	–
King mackerel	–	0.636	–	–	–
Little tunny	–	0.600	–	–	–
Other snapper	0.582	–	–	–	–
Red drum	–	–	–	0.589	–
Red snapper	0.613	–	–	–	–
Sharks	–	–	–	–	0.350
Silver/sand seatrout	–	−0.401	0.671	–	–
Spanish mackerel	–	0.600	–	–	–
Spotted seatrout	−0.474	–	–	–	–
Eigenvalue	2.248	1.691	1.448	1.235	1.141
Proportion of variance explained	0.134	0.103	0.082	0.073	0.065
Cumulative variance explained	0.134	0.236	0.319	0.392	0.457

Table 4

Significant variables of a multiple regression of spotted seatrout ln(CPUE + 1) from logbook participants, March 1987–March 1988, based on physical, temporal, geological, meteorological, and angler characteristic variables and their interactions.

Variable	b value	Partial r^2
Water depth	−0.03	0.230
Surface area × volume	-1.1×10^{-8}	0.168
Water depth × volume	1.6×10^{-7}	0.162
Water depth × surface area	2.2×10^{-6}	0.132
Number of legs	0.01	0.060
Surface area	-5.7×10^{-5}	0.038
Echosounder presence	−0.21	0.037
Fishing method	−0.26	0.033
Quadratic data	−0.01	0.025
Boat length	0.08	0.017
LORAN presence	−0.17	0.012
Engine horsepower	-7.2×10^{-4}	0.008
Structure in production	−0.14	0.006
Number of legs × wells	-2.7×10^{-4}	0.006
Number of wells	–	N.S.
Volume	–	N.S.
Intercept	0.93	
Model r^2	0.42	

N.S. = not significant at the 1% level.

number of legs × number of wells, and whether the structure was in production; and coefficients were positive for the number of legs, water depth × submerged surface area, and water depth × volume of water enclosed. Since the regression coefficients were negative for water depth, fishing method, quadratic date, boat horsepower, and the presence of LORAN and echosounder, catch rates of spotted seatrout were highest while bottom-fishing by relatively small vessels without sophisticated electronics. Based on the plot of the sum of the linear and quadratic components of month, spotted seatrout were most abundant in the late spring and early summer (Fig. 1).

Multiple-regression analysis suggested reef fish were most abundant near large complex structures at intermediate water depths (Fig. 2). Ten significant predictor variables accounted for 35.2% of the variance in the reef fish factor (Table 5). The regression coefficients of water depth, volume of water enclosed, and the interactions of submerged surface area × volume of water enclosed, and the number of legs × number of crossmembers were positive, while negative regression coefficients were observed of the interactions of water depth × volume of water enclosed, and water

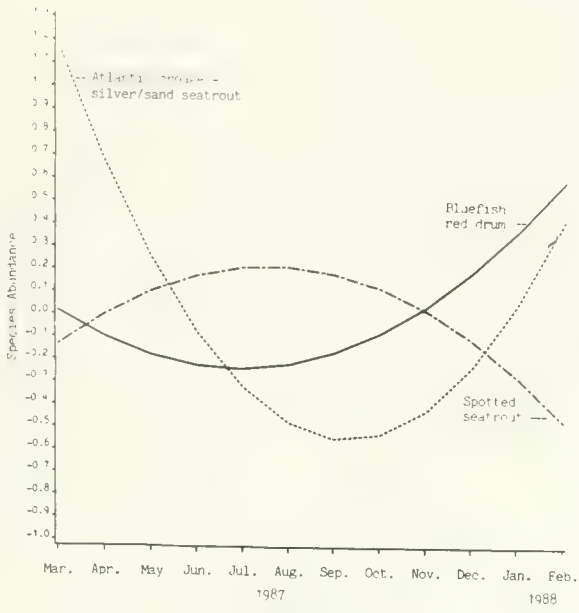

Figure 1

Calculated values of Atlantic croaker–silver/sand seatrout, bluefish–red drum, and spotted seatrout abundance on orthogonal of month from multiple regressions.

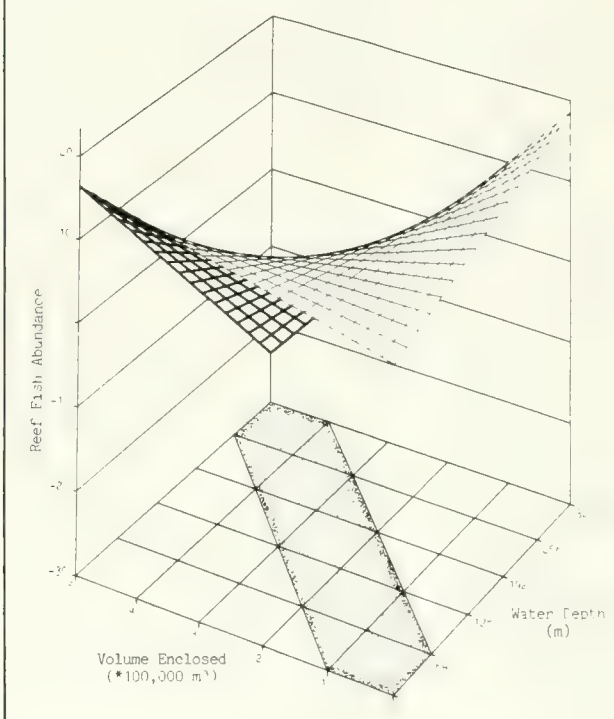

Figure 2

Response surface plot of water depth, volume of water enclosed by oil and gas platforms, and reef fish abundance from the multiple regression of principal component scores for catch data from logbook participants. Note: stippled area represents realistic values of volume of water enclosed at various depths for oil and gas platforms.

depth × submerged surface area (Table 5). Platform age did not affect the abundance of reef fish as evidenced by the negative regression coefficient for quadratic age of the platform (Table 5). Angler characteristics were not good predictors of reef fish catches, with only the presence of graph recorders and fishing method being significant (Table 5). Since the regression coefficient of fishing method was negative, reef fish catches were highest while bottom fishing.

Catches of pelagic fish were higher while trolling in relatively small, well-equipped vessels near large unmanned structures in intermediate water depths (Fig. 3). Retention of 10 significant predictor variables accounted for 31.5% of variance in the pelagic fish factor (Table 5). Regression coefficients for fishing method, LORAN presence, linear date, submerged surface area, water depth, and the interaction of submerged surface area and volume of water enclosed were positive from the MRA, while negative regression coefficients were found for the interactions of structure manned × structure in production, water depth × submerged surface area, and water depth × volume of water enclosed and boat length (Table 5).

Highest abundances of Atlantic croaker and silver/sand seatrout were found near small, manned platforms in deep water. Angler characteristic variables had little influence on their catch rates. Eight significant predictor variables explained 18.4% of the Atlantic croaker–silver/sand seatrout factor (Table 5). Temporal variables (quadratic date and linear date) had the highest partial r^2 values (Table 5) and indicated Atlantic croaker–silver/sand seatrout were most abundant in the early spring (Fig. 1). Positive regression coefficients were found for water depth and the interaction of structure manned × structure in production, and negative regression coefficients were found for volume of water enclosed and structure age × submerged surface area. LORAN presence and fishing method were the only significant angler characteristic variables retained in MRA (Table 5).

Based on MRA results, highest catches of bluefish and red drum occurred while trolling from late winter to early spring near platforms with complex construction. Retention of five significant predictor variables explained 14.5% of the variance in the bluefish–red drum factor (Table 5). The positive regression coefficient and the high partial r^2 (Table 5) for the interac-

Table 5

Significant variables of multiple regressions of reef fish, pelagic fish, Atlantic croaker–silver/sand seatrout, bluefish–red drum, and blue runner–shark–cobia principal-component scores from logbook participants, March 1987–March 1988, based on physical, temporal, geological, meteorological, and angler characteristic variables and their interactions.

	Reef fish		Pelagic fish		Atlantic croaker–silver/sand seatrout		Bluefish–red drum		Blue runner–shark–cobia	
Variables	b value	Partial r^2	b value	Partial r^2	b value	Partial r^2	b value	Partial r^2	b value	Partial r^2
Water depth	0.04	0.17	0.02	0.03	0.01	0.01	—	—	−0.01	0.04
Surface area × volume	1.6×10^{-9}	0.12	1.1×10^{-9}	0.05	—	—	—	—	—	—
Water depth × volume	-3.2×10^{-7}	0.08	-1.1×10^{-7}	0.04	—	—	—	—	—	—
Water depth × surface area	-2.3×10^{-6}	0.06	-1.8×10^{-6}	0.04	—	—	—	—	—	—
Number of legs	−0.01	0.01	−0.01	0.04	—	—	—	—	—	—
Surface area	—	—	5.5×10^{-5}	0.02	—	—	—	—	2.4×10^{-5}	0.02
Echosounder	—	—	—	—	—	—	−0.19	0.01	−0.21	0.01
Fishing method	−0.51	0.06	1.13	0.20	0.35	0.02	0.45	0.04	−0.39	0.03
Quadratic date	—	—	—	—	0.02	0.08	0.01	0.01	—	—
Boat length	—	—	−0.07	0.03	—	—	—	—	—	—
LORAN presence	—	—	0.43	0.04	−0.33	0.02	—	—	—	—
Number of legs × crossmembers	2.5×10^{-5}	0.02	—	—	—	—	1.9×10^{-5}	0.08	—	—
Graph recorder	−0.23	0.02	—	—	—	—	0.23	0.01	0.17	0.01
Quadratic age of platform	-2.8×10^{-6}	0.01	—	—	—	—	—	—	—	—
Volume	1.8×10^{-5}	0.01	—	—	-3.5×10^{-6}	0.01	—	—	—	—
Linear date	—	—	0.04	0.03	0.04	0.03	—	—	−0.02	0.01
Structure manned × production	—	—	−0.14	0.01	0.11	0.01	—	—	—	—
Age × surface area	—	—	—	—	-2.4×10^{-7}	0.01	—	—	—	—
Intercept	−0.51		−0.11		−0.11		0.45		0.31	
Model r^2	0.35		0.32		0.18		0.15		0.12	

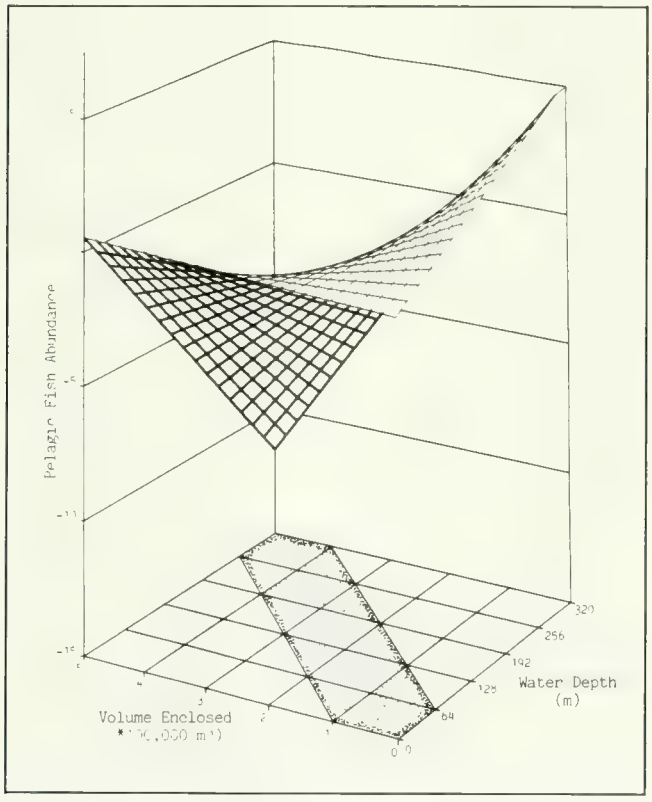

Figure 3

Response surface plot of water depth, volume of water enclosed by oil and gas platforms, and pelagic fish abundance from the multiple regression of principal component scores for catch data from logbook participants. Note: stippled area represents realistic values of volume of water enclosed at various depths for oil and gas platforms.

tion of the number of legs × number of crossmembers indicated that bluefish and red drum were most abundant near platforms with complex construction. Based on the plot of the orthogonal components of month, bluefish and red drum catch rates were highest in the early spring and late winter (Fig. 1). A positive regression coefficient for fishing method and negative regression coefficients for the presence of echosounders and graph recorders (Table 5) indicated that highest catches of bluefish and red drum occurred while trolling and that sophisticated electronic equipment did not increase catch rates.

Shark and cobia catches were highest while bottom fishing in the spring near large platforms in shallow water. The MRA with six significant predictor variables accounted for 11.5% of the variance in the shark–cobia factor (Table 5). The negative regression coefficient for water depth and positive regression coefficient for submerged surface area (Table 5) provide evidence that shark and cobia abundances were highest in shallow waters near large structures. Highest catches of shark and cobia occurred while bottom fishing in the spring, based on the negative regression coefficient for fishing method and linear date (Table 5). Conflicting results on the presence of electronic gear were found with a positive regression coefficient for presence of graph recorders and a negative regression coefficient for the presence of echo sounders (Table 5).

Discussion

Anglers and charterboat operators utilized the entire range of sizes and operational types of platforms available off the coast of Louisiana (single-well caissons, steel template platforms, and mobile semisubmersible drilling platforms), although certain trends in platform size utilization and fishing method were evident. Nearshore fishermen most often fished at the small structures (i.e., caissons) in shallow water (i.e., <10 m), while offshore bottom-fishing and trolling fishermen fished near much larger steel template platforms in deeper water (i.e., >30 m). Charterboat operators had larger vessels and were able to fish in deeper waters and farther offshore than anglers.

Anglers and charterboat operators caught a total of 36,839 fish representing at least 46 different species, providing evidence for the high diversity of fish around the oil and gas platforms. Fishes caught ranged from relatively common and highly desirable species such as spotted seatrout and red snapper to relatively rare fishes such as hake, bearded brotula, and squirrel fish. Highly sought-after gamefish such as tarpon, blue marlin, king mackerel, and yellowfin tuna were also caught. Catches by angling are selective and biased towards larger species because of the hook-and-line gear utilized, and usually only carnivorous species are susceptible to the gear. Consequently species not susceptible to angling were not represented (Grimes et al. 1982).

The associations of fish identified by the reef fish and pelagic fish PC's were in agreement with fish classification systems using direct observation around natural and artificial reefs in the Gulf of Mexico by Starck (1968) and Lukens (1981). This confirms that these groupings have an ecological basis, and were not an artifact of the sampling or analysis techniques.

Factors affecting the abundances of fish

Physical platform variables Generally, the highest abundances of spotted seatrout were found in shallow water (i.e., <10 m) around small, non-producing platforms such as caissons. These results were expected, as this estuarine-dependent species (Johnson and Seaman 1982) would likely have its highest abundances in shallow water near estuaries.

Our results suggest that reef fish, Atlantic croaker, and silver/sand seatrout abundances increased with size and complexity of the artificial reef, agreeing with past studies (Turner et al. 1969, Grove and Sonu 1983). However, an optimal artificial reef size occurred for reef fish based on the response surface plot of water depth, volume enclosed, and fish abundance as highest reef-fish abundances occurred at intermediate depths (i.e., 70–100 m) near relatively large platforms (i.e., mean volume enclosed 150,000–250,000 m^3). The optimal size range of oil and gas platforms acting as artificial reefs was significantly larger than the optimal artificial reef sizes reported in past studies. This difference could be due to the open construction and lack of interstitial spaces on oil and gas platforms which may not be as efficient at attracting or increasing secondary production of fish as the large rubble or prefabricated artificial reef units on which past estimates were calculated. Also, oil and gas platforms extend throughout the entire water column, and because many reef fish are demersal, a large portion of the platform may not be suitable reef-fish habitat. Reef-fish abundances were lowest at the largest platforms in extremely deep water, probably because the water depths exceeded the preferred ranges for these species.

Physical platform variables were not important predictor variables of pelagic fish abundance. Our results are consistent with Wickham et al. (1973) and Grove and Sonu (1983) who concluded that pelagic fishes respond to the visual attraction of artificial reefs and not to the overall size or surface area.

Bluefish, red drum, cobia, and shark abundances were highest around large, structurally complex platforms. These species were probably not trophically dependent on the structures, but were attracted to platforms by an optical stimulus as reported by Wickham et al. (1973) for cobia.

Age of the structure was not a significant factor in explaining fish composition or abundance around oil and gas platforms. Therefore it appears that the species-equilibrium model, which suggests that the number of species present and their abundances increase rapidly over a colonization period eventually stabilizing (MacArthur and Wilson 1967), was not applicable, or that the platforms may have been fully

colonized at the start of the study and we were sampling after species stabilization occurred. The latter explanation seems most likely, because the age of platforms in our study ranged from 8 months to 30 years, and full colonization of artificial reefs in the northern Gulf of Mexico can occur in as little as 15 months (Lukens 1981).

Seasonal variation Season was an important factor affecting the abundances of fish around oil and gas platforms. Smith (1979) and Lukens (1981) reported large fluctuations in species composition and abundance around natural and artificial reefs in the northern Gulf of Mexico, and based on our results this would include fish populations around oil and gas platforms off the Louisiana coast.

The apparent higher abundances of spotted seatrout in the spring and summer may be a result of a temperature-induced increase in feeding rate and/or the aggregation of the fish into spawning schools (Johnson and Seaman 1982).

The increase in pelagic fish catches from winter through fall indicated that abundance may have been related to water temperature. This is consistent with the findings by Fable et al. (1981), as they found that the charterboat catches of king mackerel and other pelagic species in the northeast Gulf of Mexico increased with water temperature.

Lassuy (1983) reported that Atlantic croaker abundance was highest in the spring and summer, while Sutter and McIlwain (1982) reported silver/sand seatrout abundance to be highest in the winter and spring. This may explain the apparent conflicts in the results from the MRA with respect to seasonal abundances of these two species. Silver/sand seatrout may have been abundant in the winter and spring, and Atlantic croaker in the spring and summer. However, when these species were grouped the seasonal abundance results explained only silver/sand seatrout and not the entire group.

Our results, along with those of others (Gallaway et al. 1981b, Reagan 1982) provided evidence that bluefish and red drum were seasonal transients with highest abundances from fall through spring. Shark and cobia abundances appeared to be highest in the spring and decreased thereafter.

Angler characteristic variables Overall, fishing power was not equal because fishermen with larger vessels and engines had access to deeper water, and fishermen with sophisticated electronics could more easily locate fish. Because reef fish, Atlantic croaker, and silver/sand seatrout are found in deep water, anglers with large vessels and engines had the highest catches for these species, while cobia, sharks, and pelagic species were more frequently caught by vessels having sophisticated electronics. Since spotted seatrout were found in shallow water, large vessels or sophisticated electronics did not increase spotted seatrout catches.

Geological and meteorological variables Geological and meteorological variables were not significant predictors of fish abundance around oil and gas platforms. Meteorological variables were probably not important because fishermen generally fish only in good weather, consequently catch rates during poor weather conditions were not reported.

Conclusions

The physical construction of oil and gas platforms precludes sampling of the associated sportfish populations using traditional methods (e.g., gillnets, trawls). Based on the results of this logbook program, the collection of CPUE data over long periods of time may be an effective technique of monitoring the fish populations susceptible to angling associated with artificial reefs. Although the data supplied by the logbooks is an index of relative abundance of fish susceptible to angling and is biased towards larger individuals, it provides a valuable source of data which is otherwise difficult to obtain.

With the advent of the "Rigs to Reefs" initiative in Louisiana, biological criteria to determine where to locate retired oil and gas platforms as artificial reefs was needed. Information derived from this study suggests that optimal artificial reef configurations exist, but vary depending on the species. To effectively site artificial reefs for reef fish, Atlantic croaker, and silver/sand seatrout there should be large complex platforms at intermediate depths; for pelagic species artificial reef size is not a factor, although they should again be placed at intermediate depths. Optimal siting of artificial reefs for spotted seatrout should include small structures in shallow water. Gallaway and Lewbel (1982) suggested that abundances of some species were directly proportional to the submerged surface area of oil and gas platforms. We believe that the relationship between fish abundances and artificial reefs is much more complex, with other factors, such as natural and temporal variability of species distribution and abundance interacting with physical platform variables and water depth to determine overall species abundances.

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Abstract.—Serum progesterone and testosterone levels, as measured by radioimmunoassay, were used to estimate the mean length at attainment of sexual maturity (LSM) in a sample of 124 female and 31 male incidentally-killed Dall's porpoises *Phocoenoides dalli*. Females with serum progesterone levels greater than 1.34 ng/mL were considered mature. The LSM for females was estimated at 169.0 cm using Kasuya's "summation" technique. A technique to fit a two-phase regression model to the male data produced an estimated LSM for males of 183.0 cm. Overall, the estimates for the LSM in this study agreed well with previously published reports using histological and morphological measures of sexual maturity. Hormonal estimation of maturity is proposed as a rapid, inexpensive, and potentially non-lethal alternative technique in odontocete populations.

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Use of Serum Progesterone and Testosterone to Estimate Sexual Maturity in Dall's Porpoise *Phocoenoides dalli*

Jonathan L. Temte

Hatfield Marine Science Center, Oregon State University, Newport Oregon 97365
Present address: Department of Zoology, University of Wisconsin
Madison, Wisconsin 53706

Estimation of the mean age and length at the attainment of sexual maturity in odontocetes has traditionally relied upon morphological or histological parameters, thus necessitating whole animal preparations. Examination of reproductive tissue allows for the determination of maturity. When this information is coupled with age/length data, the age or length at attainment of sexual maturity for females and males in a population can be determined using a variety of methods (DeMaster 1984). These methods, however, implicitly require the collection of dead marine mammals in the field.

Several authors have used radioimmunoassay (RIA) to assess reproductive condition in living odontocetes. For example, RIA of progesterone has been used as an indicator of luteal function in *Tursiops truncatus*, *Delphinus delphis* (Kirby and Ridgway 1984, Sawyer-Steffan et al. 1983), and *Stenella longirostris* (Wells 1984). Likewise, measurements of serum testosterone by RIA have been used to assess male sexual condition in *T. truncatus* (Harrison and Ridgway 1971) and *S. longirostris* (Wells 1984).

Temte and Spielvogel (1985) demonstrated that serum progesterone concentration, as measured by RIA, was a good predictor of corpus luteum mean diameter in a sample of 32 incidentally-killed pregnant or lactating Dall's porpoises *Phocoenoides dalli* from the northwestern North Pacific Ocean. Furthermore, they noted that 17 sexually immature females (no corpora present in ovaries) had very low concentrations of serum progesterone (Table 1).

In this study the results of progesterone and testosterone RIA in 124 female and 31 male Dall's porpoises, respectively, were used to estimate the mean length at attainment of sexual maturity (LSM) in this species. The results are compared to those obtained using traditional histological techniques to demonstrate the effectiveness of this inexpensive and nonlethal technique.

Methods

Blood samples

During June and July of 1982, personnel of the National Marine Mammal Laboratory (NMFS) obtained blood samples from a total of 105 Dall's porpoises that were incidentally-killed in Japanese salmon gillnets in the North Pacific Ocean. The following groups were represented in the sample: 21 non-pregnant, nonlactating females in which the maturity status was not known (149–199 cm, standard body length); 30 pregnant females (167–200 cm); 23 lactating females (167–200 cm), and 31 males in which the maturity status was not known (101–210 cm). Samples of whole blood were drawn and centrifuged using methods described

Table 1

Serum progesterone concentrations [P] in immature and mature female Dall's porpoises. Data from 1980 sample of Temte and Spielvogel (1985).

Status	No.	Mean [P] (ng/mL)	SD	Range of [P]
Mature	33	14.76	12.43	0.0–45.3
Pregnant (P)	24	19.40	11.31	0.9–45.3
Lactating (L)	8	2.63	3.75	0.0–11.4
non-P, non-L	1	0.49		
Immature*	17	0.27	0.46	0.0–1.3

* Excluding one immature female with a large follicle and 31.1 ng/mL progesterone.

by Temte and Spielvogel (1985). In these samples, however, serum was decanted into 1.5-mL plastic ultracentrifuge tubes and frozen at −20°C until assays were performed.

RIA for progesterone

Progesterone RIA was identical to that reported by Temte and Spielvogel (1985). This assay had previously been validated for porpoise serum, and chromatography had shown an absence of interference from other serum constituents. Triplicate volumes of porpoise serum (10 μL for pregnant, 50 μL for lactating, and 100 μL for non-pregnant, non-lactating females) were doubly extracted utilizing a 1:2 mixture of benzene and hexane (Sawyer-Steffan and Kirby 1980). The antiserum used was anti-progesterone-11-BSA, No. 1337 (Gordon D. Niswender). The intraassay coefficient of variation (COV) was 5.5%, while the interassay COV was 5.9%. The sensitivity of this assay was 0.1 ng/mL.

RIA for testosterone

The procedure for testosterone RIA was nearly identical to that for progesterone. Triplicate volumes of 25-μL porpoise serum were doubly extracted with 1:2 benzene:hexane. The antiserum used was anti-testosterone, No. s-250 (Gordon D. Niswender). The competitor was [^{3}H]testosterone (NET-553, New England Nuclear). The intraassay coefficient of variation (COV) was 6.3%, while interassay COV was 14.6%. The assay sensitivity was 0.3 ng/mL.

Maturity criteria for females

The mean serum progesterone for immature females reported in Temte and Spielvogel (1985) was 0.27 ng/mL. Assuming a normal distribution, 99% of immature females would be expected to have serum progesterone levels less than 1.34 ng/mL. Based upon this result, females with serum progesterone concentrations greater than 1.34 ng/mL were considered sexually mature. Whereas, this progesterone level is lower than the 3.0 ng/mL used by Kirby and Ridgway (1984) as an indicator of ovulation in *D. delphis* and *T. truncatus*, 94% of the immature females and 96% of the pregnant females reported in Temte and Spielvogel (1985) were correctly classified using this criteria.

Maturity criteria for males

Since samples were collected near the peak breeding period for Dall's porpoises (Newby 1982; see also Jefferson 1989), and considering the seasonal flux of testosterone in other odontocetes (Wells 1984), separation of immature and mature Dall's porpoises by testosterone level alone was theoretically possible in this study. Although Wells (1984) regarded serum testosterone concentrations of less than 8.0 ng/mL as baseline levels in *S. longirostris*, a natural break in the Dall's porpoise data occurred between 1.7 and 5.0 ng/mL. However, as tissue samples were not available for maturity assessment, no hormonal maturity criteria could be confirmed.

Estimation of LSM

The proportions of mature females in each 10-cm increment (135–225 cm) were calculated. Graphical analysis determined the length at which the cumulative probability of maturity, $\Sigma(m_i)$, equaled the cumulative probability of not being mature at that length or longer, $\Sigma(1-m_i)$. This method was first used by Kasuya (1972) and has been termed the summation technique by DeMaster (1984). It is recommended when small samples of size- or age-classes exist.

A small total sample precluded the use of the summation technique in males. As a consequence, a modification of the regression technique (see DeMaster 1984) was used to identify the LSM. Because testosterone concentrations demonstrated a discontinuity (see above), a continuous two-phase regression model (Yeager and Ultsch 1989; review by Nickerson et al. 1989) was used to objectively identify the transition point in the data. The transition point in the length represents the point at which the discontinuity occurred, or in this case, the LSM.

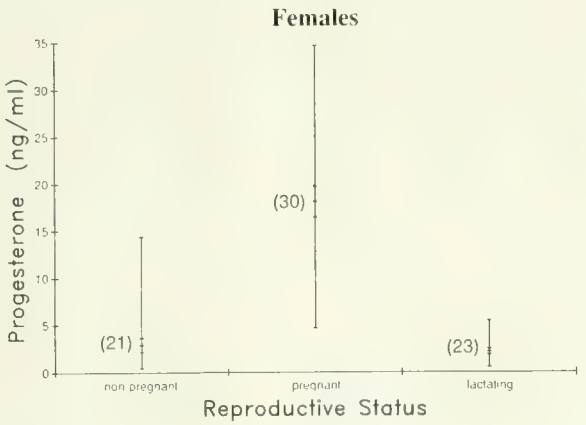

Figure 1
Serum progesterone concentrations for non-pregnant/non-lactating, pregnant, and lactating female Dall's porpoises. Vertical bars indicate ranges of values. Horizontal bars indicate means and standard errors. Sample sizes are in parentheses. Animals were collected June–July 1982 in the western North Pacific Ocean.

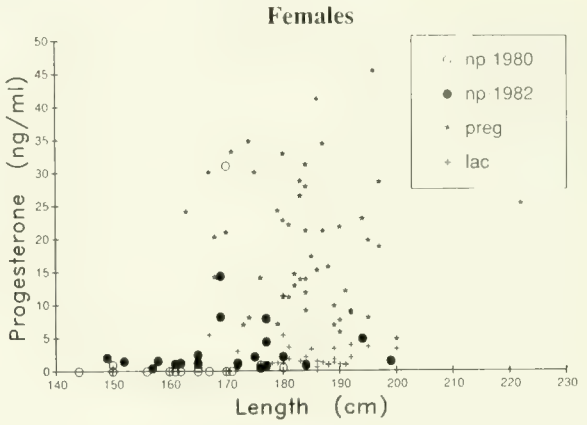

Figure 2
Serum progesterone concentration as a function of length in non-pregnant (1980 O; 1982 ●), pregnant (*), and lactating (+) female Dall's porpoises.

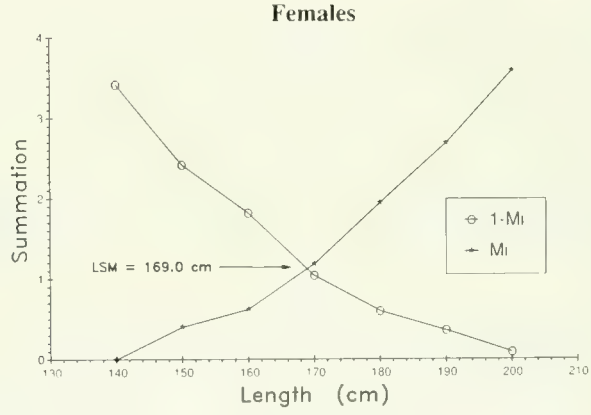

Figure 3
Summation technique for female Dall's porpoises based on progesterone values. Intersection of lines occurs when $\Sigma(m_i) = \Sigma(1-m_i)$.

Results

Comparison of 1982 and 1980 progesterone data

The results of the progesterone assays (1982 data: Fig. 1) were compared with results of Temte and Spielvogel (1985) (1980 data). No significant differences were found between the mean progesterone concentrations for pregnant females (1980: $n = 24$, $\bar{x} = 19.40$; 1982: $n = 30$, $\bar{x} = 18.09$; $P > 0.5$; Student's t-test), or for lactating females (1980: $n = 8$, $\bar{x} = 2.63$; 1982: $n = 23$, $\bar{x} = 2.17$; $P \gg 0.05$; Wilcoxson rank sum). Mean progesterone concentrations were significantly different for the two groups of non-pregnant, non-lactating porpoises (1980: $n = 19$, $\bar{x} = 1.91$; 1982: $n = 21$, $\bar{x} = 2.92$; $P < 0.01$; Wilcoxson rank sum). However, the mean length of the 1982 sample was significantly greater than that of the 1980 sample (1982: $\bar{x} = 171.2$ cm; 1980: $\bar{x} = 163.1$ cm; $P < 0.05$; Student's t-test), and the difference in mean progesterone could be due to a difference in the proportion of mature females. Therefore, the results of progesterone analysis in pregnant, lactating, and non-pregnant/non-lactating females from the 1982 sample were pooled with the results from the 1980 sample of Temte and Spielvogel (1985).

Females

Serum progesterone is plotted against length for 124 female Dall's porpoises (Fig. 2). The results demonstrate the incidence of high progesterone levels at lengths greater than 165 cm. These elevated levels were seen not only in pregnant females, but also in non-pregnant, non-lactating females, indicating possible ovulation. The summation technique provided an estimated LSM of 169.0 cm (Fig. 3).

Males

Serum testosterone displayed a marked increase with an increase in length. A natural break in the testosterone data occurred between 175 and 180 cm, when

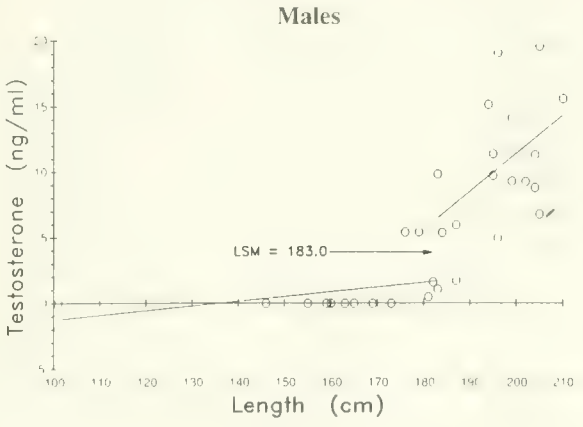

Figure 4

Serum testosterone concentration as a function of length for 31 male Dall's porpoises collected in 1982. Two-phase regression lines are shown.

testosterone increased from undetectable levels to relatively high levels. The best fitting two-phase regression model (Fig. 4) indicated that the transition point occurred at 183.0 cm. Hence, the LSM for males was estimated as 183.0 cm. The mean (± SE) testosterone concentration was 1.00 ± 0.52 ng/mL for males shorter than the LSM, and 10.46 ± 1.20 ng/mL for males longer than the LSM.

Discussion

Newby (1982), using the presence of ovarian scars and the 50th percentile method (see DeMaster 1984), estimated the LSM to be 170.5 cm for females in this western North Pacific population. The use of hormonal data alone provided a similar, but slightly lower, LSM estimate of 169.0 cm. However, based on the growth curves for females of this population (fig. 31 in Newby 1982), this 1.5-cm difference translates into small differences in ages.

The estimate for LSM in males of 183.0 cm is in very close agreement with the previously estimated LSM of 182.6 cm based on the 50th percentile method using testis-epididymal weight (Newby 1982). Direct comparison with previous studies are not possible due to the lack of variance estimates for LSM by the methods used. Nevertheless, the hormonal estimates of LSM provided in this study agree quite well with previous, non-hormonal methods.

Radioimmunoassay is a quick, economical, and accurate measure of reproductive condition. Small samples of blood (<1 mL) provide adequate serum for replicate assays. Previous studies have shown the high predictive value of serum progesterone level to corpus luteum size and reproductive state (Temte and Spielvogel 1985, Kirby and Ridgway 1984, Sawyer-Steffan et al. 1983). Moreover, such methods could allow the rapid collection of samples for maturity status assessment from large numbers of animals in the field.

Hormonal assessment of reproductive status may prove to be a non-lethal technique to estimate population parameters such as LSM. It is, at present, more applicable to captive animal studies. However, situations in which animals are killed incidentally may provide opportunities for obtaining concordant blood and reproductive tissue samples. Such sampling could allow the direct comparison of hormonal and histological methods of estimating maturity and establish appropriate hormonal criteria for future studies.

Seasonality in breeding may well limit the usefulness of this method in males (see Perrin and Donovan 1984) because testosterone undergoes seasonal fluctuation. In addition, the presence of environmental toxins may interfere with steroid hormone production. For example, Subramanian et al. (1987) have shown a significant negative relationship between testosterone concentration and DDE residue level.

There is potential for using progesterone, testosterone, and other hormonal parameters, such as chorionic gonadotropin, FSH, and LH, in the estimation of sexual maturity and reproductive status in marine mammal populations. As we expand our reproductive database in the cetacea, we also need to correlate histological and morphological states with hormonal parameters. Research protocols which include 10-mL samples of fresh blood and assessment of hormonal state should be encouraged.

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Detecting Differences in Fish Diets

David A. Somerton

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA, 2570 Dole Street
Honolulu, Hawaii 96822-2396

Statistical comparison of the diet of a predator between areas or time-periods allows one to distinguish true dietary differences from sampling variability and may lead to a better understanding of a species' feeding habits. Despite the utility of statistical testing, few procedures appropriate for dietary comparisons have been developed. Perhaps one impediment to the development of a general approach to dietary comparisons is the wide variety of ways in which diets have been expressed and the lack of consensus about which is best. For example, diets expressed as the numeric or gravimetric proportions of the total food consumed will require different approaches to statistical comparison than those expressed either as the proportion of the samples containing each of the various prey types, or as the index of relative importance of each prey type (Pinkas et al. 1971).

For cases in which diets are expressed in terms of gravimetric proportions, Crow (1979) and Ellison (1979) have recommended statistical tests of between-sample differences based on multivariate analysis of variance (MANOVA). Validity of such tests, however, requires that the prey proportions have a multivariate normal distribution and that the variance-covariance structure of the prey proportions is identical among samples (Morrison 1976). Recognizing that dietary data are unlikely to have these properties, Crow (1979) further recommended using MANOVA that incorporates non-parametric procedures. Herein, this recommendation is followed, and a new approach for testing differences in diets using non-parametric MANOVA is examined. This approach combines the usual measure of between-sample differences employed in parametric MANOVA (i.e., Hotelling's T^2 statistic; Morrison 1976) and a non-parametric procedure (i.e., a randomization test; Edgington 1987) to determine the significance of T^2. The method is then applied to determine whether the diet of pelagic armorhead *Pseudopentaceros wheeleri* from the Southeast Hancock Seamount changed between two sampling periods.

Materials and methods

Testing for between-sample differences is accomplished in three steps: (1) calculating for each sample the gravimetric dietary proportions and their variances and covariances, (2) calculating a measure of the statistical difference between samples, and (3) determining the statistical significance of the measure. The gravimetric proportion of the diet contributed by prey category j(p_j) can be estimated as the total weight of prey category j in all stomach samples divided by the total weight of all prey categories combined (Hyslop 1980). Algebraically this is expressed as

$$p_j = \frac{\sum_k w_{jk}}{\sum_j \sum_k w_{jk}} = \frac{w_{j.}}{w_{..}} \qquad (1)$$

where w_{jk} is the weight of prey category j for individual k, $w_{j.}$ is the total weight of prey category j summed across all individuals, and $w_{..}$ is the total weight of all prey. Each p_j is transformed to x_j, where $x_j = \arcsin \sqrt{p_j}$, so that it conforms more closely to a normal random variable (Sokol and Rohlf 1969). Because x_j is estimated as a pooled proportion rather than the average of the proportions for individual fish, the variance of x_j and the covariance between x_j and x_i cannot be calculated directly and instead are approximated by using the delta method (Seber 1973). In the following, $\mathbf{x}_i$ indicates the vector of x_j for sample i, and $\mathbf{S}_i$ indicates the matrix of variance and covariance estimates for $\mathbf{x}_i$.

The measure of statistical difference used is the Hotelling's T^2 statistic, a multivariate extension of the t-statistic (Morrison 1976). In matrix notation, this statistic is expressed as

$$T^2 = (\mathbf{x}_1 - \mathbf{x}_2)' \, \mathbf{S}_{\cdot}^{-1} \, (\mathbf{x}_1 - \mathbf{x}_2), \qquad (2)$$

where $\mathbf{S}_{\cdot}^{-1}$ is the inverse of the pooled estimate of the variance-covariance matrix (Morrison 1976). $\mathbf{S}_{\cdot}$ is approximated, assuming reasonably large sample sizes (>50 stomachs with prey per sample), as

$$\mathbf{S}_{\cdot} = \frac{2(N_1 \mathbf{S}_1 + N_2 \mathbf{S}_2)}{N_1 + N_2}, \qquad (3)$$

where N_1 and N_2 are the sizes of the two samples.

Once a value of T^2 is computed, its significance is determined from an empirical probability distribution of T^2 computed by using a technique known as randomization (Edgington 1987). Computation of the empirical probability distribution using this technique proceeds as follows: (1) stomach content data from both time or area samples are

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Table 1

Probability levels associated with the randomization tests of the individual hypotheses. Because these are *a posteriori* tests, significance levels were adjusted according to the Bonferroni inequality to 0.25α ($^{*}P \leq 0.0125$, $^{**}P \leq 0.0025$).

	Mean proportion			
	Sample 1	Sample 2	t-value	Probability level
Tunicates	0.32	0.69	−9.1	$<0.001^{**}$
Crustaceans	0.27	0.13	5.0	0.011^{*}
Fish	0.26	0.10	3.7	0.046
"Others"	0.15	0.08	1.9	0.294

combined, (2) the combined data are randomly sorted into two new samples equal in size to the originals, and (3) a value of T^2 is calculated for the two samples. Steps 2 and 3 are repeated iteratively (the present study uses 5000 iterations), and the probability distribution of the randomized values of T^2 is then calculated. Next, the significance level of obtaining the original T^2 is estimated by determining the proportion of the randomized T^2 values that, ignoring signs, is equal to or greater than the original.

If between-sample equality of the diet is rejected, it is then appropriate to test for the equality of individual prey categories to determine which categories contribute most to the difference in diet. In this case, the measure of statistical difference used is the univariate t-statistic. In matrix notation, the vector of t-statistics (**t**) can be computed as

$$\mathbf{t} = \mathbf{D}_{\cdot}^{-1}(\mathbf{x}_1 - \mathbf{x}_2), \quad (4)$$

where $\mathbf{D}_{\cdot}^{-1}$ is the inverse of a matrix formed from the diagonal elements of $\mathbf{S}_{\cdot\cdot}$. As before, the significance of each t-statistic is determined from an empirical probability distribution computed for each prey category using randomization. Computation of these probability distributions is identical to that described for the multivariate case, except that a matrix of univariate t-statistics (Eq. 4) is used in the calculation instead of the T^2-statistic (Eq. 2). These individual tests are *a posteriori* tests and require some adjustment of the error rate considered to be significant. Using the Bonferroni inequality (Morrison 1976, Miller 1981), an appropriate adjustment is to assume significance at $\alpha \cdot n^{-1}$.

The above procedures have been incorporated into the computer program DIETTEST, which is designed to run on IBM-compatible microcomputers. This program is available from the author.

As an example of the application of this method, it has been used to test for dietary differences between two samples of pelagic armorhead: 55 fish collected in June 1985, and 101 fish collected in August 1988 (only fish with prey in their stomachs were used in the analysis). Both samples were obtained from the Southeast Hancock Seamount (lat. 30°N, long. 180°W) on the Hawaiian Ridge. Stomach contents were sorted to the lowest taxonomic category possible, then blotted and weighed to the nearest milligram. To simplify the analysis, various prey items were pooled into four major prey categories: tunicates, crustaceans, fish, and "others."

Results and discussion

When the method was applied to the two armorhead samples, the test of the simultaneous equality of all dietary proportions between samples was highly significant ($P<0.001$), indicating that the diet of pelagic armorhead had changed between the two sampling periods. Because of this, tests were also made for individual prey categories. Two of the four prey categories, tunicates and crustaceans, differed significantly between samples (Table 1) and therefore appeared to be responsible for the overall difference in diet.

The measure of between-sample difference, T^2, employed in the proposed test was selected primarily because the absolute differences between samples are scaled by the within-sample variances, a particularly desirable feature when dealing with highly variable quantities such as fish diets. This choice, however, imposes a constraint on the proposed statistical test; that is, the method can only be applied to cases in which the two diet samples lack mutually exclusive components. This constraint arises because computation of T^2 requires inversion of the variance-covariance matrix (Eq. 2) which is singular and therefore not invertible when a prey category is completely absent from one of the samples. Although this constraint may not be severe when the diet of a single predator is being examined for spatial or temporal variation, especially if one is willing to accept the pooling of prey to relatively high taxa, the proposed method is likely to be of limited value for comparing the diets of different predators. For such between-predator comparisons, a more appropriate test could be developed by utilizing some measure of diet overlap (Caillet and Barry 1979) which is not affected by mutually exclusive prey categories, instead of T^2 as a measure of between-sample difference.

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Abstract.—Nine lactating northern fur seals *Callorhinus ursinus* from St. Paul Island, Alaska, were instrumented with time-depth recorders and head-mounted radio transmitters in July and August 1985. Seven females were subsequently located at least once while at sea. Diving patterns obtained from females' time-depth recorders were then associated with their foraging locations. Generally two diving patterns were found; shallow-diving and deep-diving. The deep-diving pattern appears to be associated with feeding throughout the day over the continental shelf in water less than 200 m deep. The shallow-diving pattern is generally restricted to nighttime hours and probably occurs mostly over deep water. An analysis of the occurrence of food in stomachs of lactating fur seals collected in the eastern Bering Sea from 1958 to 1974 also suggests that seals collected over the continental shelf were more likely to be feeding during the day. We examine differences in the way shallow- and deep-diving females forage and discuss possible prey associated with the two diving patterns.

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Diving Patterns and Foraging Locations of Female Northern Fur Seals

Michael E. Goebel
John L. Bengtson
Robert L. DeLong
Roger L. Gentry
Thomas R. Loughlin

National Marine Mammal Laboratory, Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE
Seattle, Washington 98115-0070

The sexually dimorphic northern fur seal *Callorhinus ursinus* is a polygynous colonial breeder. Arrival of adult females and pupping are highly synchronous; most pupping occurs between 21 June and 31 July. Females give birth to a single pup within 1–2 days after arrival at the same site each year. Copulation occurs approximately 5 days after parturition, and females remain on shore 1–2 days more before going to sea to feed (Gentry and Holt 1986). The first feeding trip is the shortest, and subsequent trips gradually become longer (Gentry and Holt 1986). Periods of feeding at sea alternate with visits ashore to suckle their pups. The period from birth to weaning is approximately 125 days.

Compared with the land phase of the fur seal's life history, little is known of their life and behavior at sea. Kooyman et al. (1976) first reported on depth and duration of dives for a lactating northern fur seal. General patterns of diving behavior for breeding females were described by Gentry et al. (1986c). They found that individual females exhibit two discrete types of diving patterns: shallow and deep. Some females, exhibiting both patterns, showed the deep-diving pattern on the first and last days of a trip and the shallow pattern on other days. Fur seals exhibiting the deep-diving pattern typically dive to depths greater than 75 m without changing depth during a diving bout and dive at all hours of the day (Gentry et al. 1986c).

Feeding locations of individuals exhibiting different diving patterns, however, were unknown. Loughlin et al. (1987) initiated studies to determine what foraging areas in the Bering Sea were critical for lactating females. In 1984 using a ship, they located 11 females equipped with radio transmitters and tracked 4 of them to foraging locations. In 1985, they located 20 females with radio transmitters at sea from aircraft.

This paper reports our efforts to link fur seal diving behavior and foraging locations by instrumenting females with both radio transmitters (to determine location) and dive recorders (measuring depth of dive). We examine differences among females in diving behavior and their patterns of foraging, and discuss how diving behavior correlates with possible prey species.

Study area and methods

This study was conducted at Zapadni Reef rookery on St. Paul Island, Pribilof Islands, Alaska, from 19 July to 16 August 1985 (Fig. 1). Nine female northern fur seals with pups were

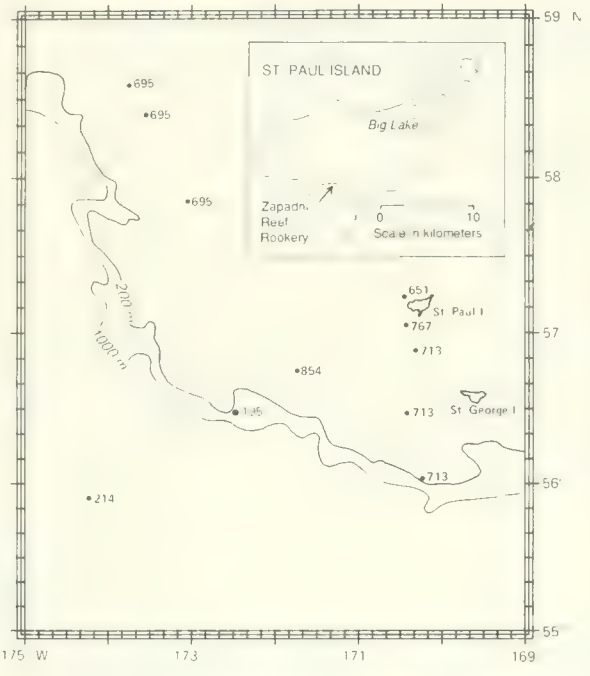

Figure 1

Study area with plotted locations of seven female northern fur seals equipped with time-depth recorders and their relation to the continental shelf break (the 200-m contour).

captured with a noose pole, removed from the rookery, and placed on a restraint board (Gentry and Holt 1982). Each female was tagged on the fore-flippers (Allflex sheep ear tag) and equipped with a radio transmitter (164 Mhz, Advanced Telemetry Systems, Isanti, MN) and a photomechanical time-depth recorder (TDR) (Meer Instruments, Solana Beach, CA). Radio transmitters were attached to the top of each seal's head with quick-setting epoxy resin (Devcon EK-40) (Loughlin et al. 1987) and TDRs were attached to seals by harness (Gentry and Kooyman 1986). After the epoxy resin had hardened (20–25 minutes), each female was returned to her capture site and released. Females were recaptured with a hoop net on their next visit ashore and the TDR was removed by cutting the harness. When possible, the mass for each female was determined at each capture.

Females were located at sea using a twin-engine airplane equipped with a two-element Yagi antenna mounted on each side of the fuselage (Loughlin et al. 1987). A total of 60 hours was flown on predetermined transects within 300km of St. Paul Island at speeds of 100–120 knots and at 1200m altitude.

Film from recovered TDRs was developed in either Agfa Rodinol or Kodak D-19. Each record was reproduced on paper with a 7× enlargement using copy flow xerography. At least three points of each dive were digitized on an electronic digitizing pad: the start, the end, and the maximum depth. These points allowed computation of dive duration, depth, and interdive surface interval. Each record was analyzed for bouts of diving using the same criteria used by Gentry et al. (1986c) for *Callorhinus*: five or more dives with less than a 40-minute surface interval between each dive.

The duration of diving bouts, number of dives per bout, percent time below the surface, and number of dives per hour were calculated as indices of the patterns of foraging.

The percent time spent below the surface was calculated separately for all dive bouts that occurred at mean depths of less than 75m and for bouts greater than or equal to 75m. An ANOVA on percent time below the surface was made after an arcsine transformation of the data. All comparisons for significant differences in depth were made using ANOVA with significance accepted at $\alpha \leq 0.05$.

The number of dives per hour was calculated for daytime (0700–2259) and nighttime (2300–0659) hours and for the entire record for each female. Percent of total dives for day and night hours was also calculated.

To further test the relationship between foraging locations and dive patterns, we used data from the National Marine Mammal Laboratory's pelagic fur seal database, which provided a large sample of lactating females that had been collected from July to September, 1958–74, from the eastern Bering Sea. We compared the proportion of stomachs with food to empty stomachs of lactating females collected over the continental shelf (<200m depth) and for those collected off the continental shelf (>200m depth; chi-square analysis). For the comparison, we used specimens obtained between the hours of 0600–1000 and 1400–1900 (we chose 0600 and 1900 because they were the start and the termination of sampling, and we arbitrarily selected 1000 and 1400).

Results

Four of the nine females (nos. 195, 566, 651, 695) instrumented with TDRs and radio transmitters were deep divers, diving at all hours of the day; the other five (nos. 214, 308, 713, 767, 854) were shallow divers and dived primarily at night (Fig. 2).

Seven of these females, three deep divers and four shallow divers, were located at sea at least once. Female 195 was located on the third day of a 12-day trip at the continental shelf break. At this location the bathymetry changes rapidly, and because aerial locations are only approximate this female could have been

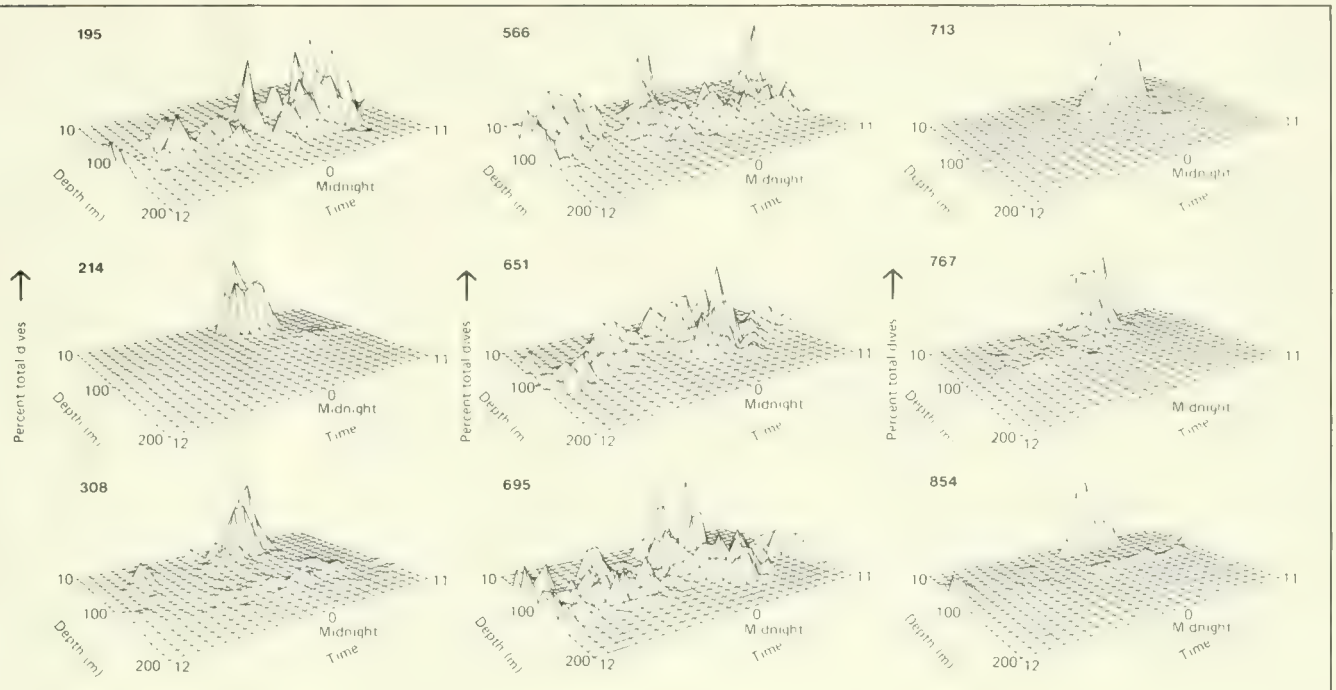

Figure 2

Three-dimensional plots of diving records for nine female northern fur seals at St. Paul Island, Alaska, in July and August 1985. Each plot represents the diving record (all dives ≥20 m in depth) of one trip to sea for each female.

in water 140 m to 1400 m deep. On the day she was located, as well as on most days of her trip, she exhibited the deep-diving pattern. For a 24-hour period from 1200 on 4 August until 1200 on 5 August she made 70 dives (50% during the day) with a mean depth of 94.2 m (SD 18.5).

Two females (651 and 767) were located only once, on their return to St. Paul from a foraging trip (Fig. 1, Table 1). Female 651 was located 2.5 hours before she returned ashore and after she had completed 99% of her foraging trip. Her last dive was 6.9 hours before being located. Female 767 was located 8.2 hours before she returned ashore and 2.5 hours after her last dive.

Female 695 was located on three separate days, each time she was 110–160 km northwest of St. Paul Island, diving to depths greater than 100 m over the continental shelf in water 110–140 m deep. This female exhibited the deep-diving pattern every day of her 10-day trip, but also made seven dive bouts which had mean dive depths of less than 75 m, five of which occurred during the night.

Female 214 was located on the fifth day of a 12-day feeding trip in approximately 3500 m of water. On that day, as well as most other days, she exhibited the shallow diving pattern and dived primarily at night (Fig. 3).

Female 713 was also located on three consecutive days. She exhibited a foraging pattern of deep diving, day and night, on the first and last days of a foraging trip and shallow diving at night on other days. She was located on 25 July, the fifth day of a 7-day trip, 80 km south of St. Paul Island at the continental shelf break in approximately 200 m of water. On that day she dived exclusively at night with a mean depth of dive of 46.7 m (SD 17.1, n 171). This was the night following her location at the shelf break. On the sixth day and on the last day of her trip she was located over the shelf and dived both during the day and night to much greater depths (mean depth of dive 101.3 m, SD 26.9, n 67 for the sixth day, and 103.5 m, SD 11.0, n 11 for the last day).

Female 854 was located on the first day of a 4-day trip over the continental shelf but within 18 km of the 200-m depth contour. From the time she left shore (2208) until she was located 20.8 hours later she had made 22 dives—all but three were greater than 75 m ($\bar{x}$ 75.6, SD 7.6). Of these dives, 77% were made before dawn. Her second night at sea was spent actively diving to depths of less than 35 m (n 70, $\bar{x}$ 22.8, SD 19.6). She began diving at 2353 and dived continuously until 0340. This female was in transit across the continental shelf during the night, making occasional dives

Table 1

Mean depth (m) of dive for a 24-hour period (1200–1200) on the date of location for seven female northern fur seals equipped with radio transmitters and time-depth recorders, St. Paul Island, Alaska, 1985.

Female ID	Date	Time	% time into trip	Depth of dive[1] $\bar{x}$	SD	N	Nearest dive[2] Depth	Nearest dive[2] Time	Approximate depth at location
Deep divers									
195	8/04	1411	21.7	94.2	18.5	70	70.5	+1.63	140–1400
651	7/28	1613	99.0	–	–	–	71.5	−7.10	50
695	7/28	1340	47.8	107.6	28.4	85	131.5	−0.45	120
	7/29	1231	56.9	103.0	36.9	51	104.0	+0.07	110
	7/30	1217	66.4	118.1	10.3	52	137.5	−0.05	120
Shallow divers									
214	8/04	1313	39.0	35.5	20.9	159	85.6	−1.57	3500
713	7/25	1758	69.7	46.7	17.1	171	60.6	+6.35	200
	7/26	1414	80.9	101.3	26.9	67	89.5	+7.40	110
	7/27	1717	96.1	103.5	11.0	11	99.5	−1.47	80
767	7/26	1113	72.8	–	–	–	45.8	−2.67	20
854	8/03	1855	23.1	39.3	18.2	78	71.5	−1.23	120

[1]Females 767 and 651 had no dives during 1200–1200 on the date of location.
[2]Depth (m) of the dive closest to the time of location and the number of hours since the time of location.

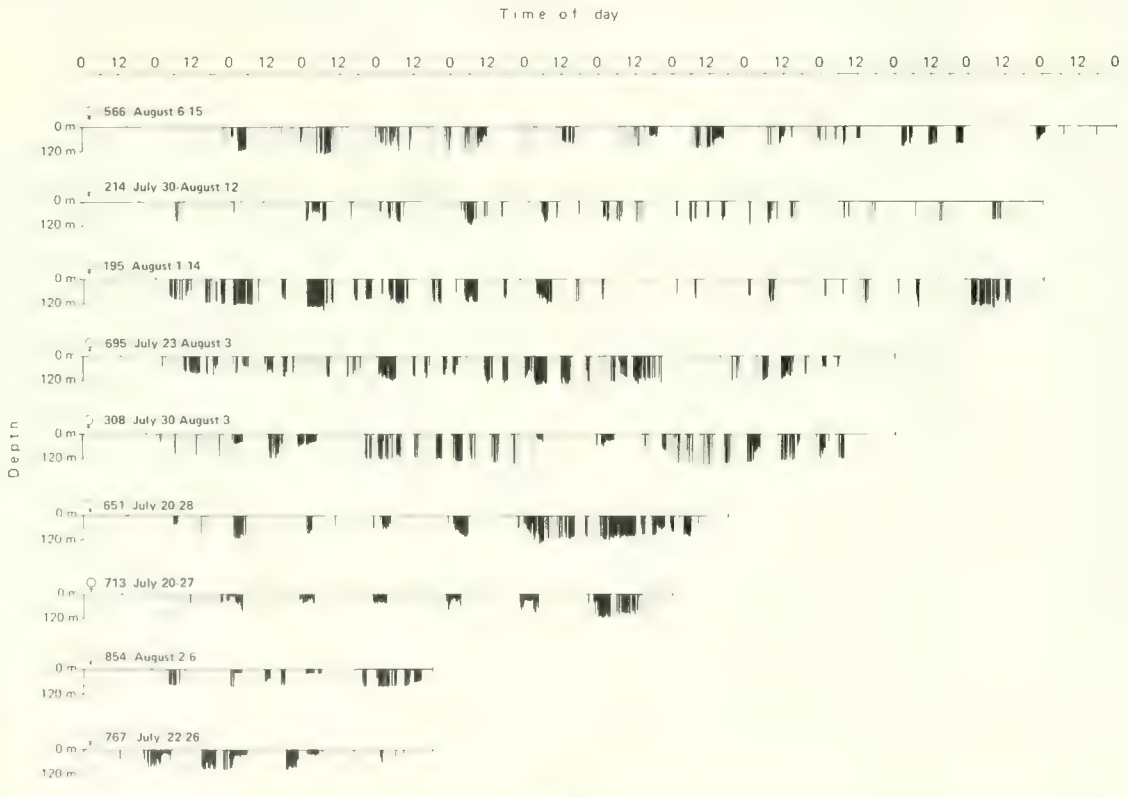

Figure 3

Two-dimensional plots of diving records for nine female northern fur seals at St. Paul Island, Alaska, in July and August 1985. Each plot represents the diving record (all dives ≥20 m in depth) of one trip to sea for each female.

Table 2

Record lengths, times to first and from last diving bouts, and mass of nine female northern fur seals instrumented with time-depth recorders in July and August 1985, St. Paul Island, Alaska.

Female ID	Start		Total hours	Time to first dive bout[1]	Time from last dive bout[2]	Mass (kg)[3]		
	Date	Time				1	2	Gain
Deep divers								
195	8/01	2308	290.22	4.72	12.25	34.0	37.6	3.6
566	8/06	1425	225.25	34.08	22.67	41.3	45.4	4.1
651	7/20	1442	196.33	14.72	12.75	31.3	33.6	2.3
695	7/23	1204	253.17	20.52	18.18	48.5	49.9	1.4
Shallow divers								
214	7/30	1820	295.42	11.87	14.63	31.3	33.1	1.8
308	7/24	2042	242.50	2.98	15.13	—	39.5	?
713	7/20	1342	178.28	23.03	8.12	—	34.0	?
767	7/22	0041	114.75	18.98	18.73	39.5	—	?
854	8/02	2208	91.01	4.65	3.00	40.1	40.4	0.3

[1] Time to first dive bout is the time from departure from shore until the first dive bout measured in hours. A dive bout is defined as any series of dives greater than five dives with surface intervals of less than 40 minutes (Gentry et al. 1986c).
[2] Time from the last dive bout (in hours) until the female returns to shore.
[3] Mass 1 is the mass taken upon deployment (the first capture), and mass 2 is the mass taken upon recapture (the second capture).

to depths greater than 75 m and then once near the shelf break, she began diving to shallow depths.

Female mass and depth of dive

Seven of the nine females were weighed at instrument deployment, and eight were weighed when the instrument was recovered (Table 2). All females weighed twice showed a mass gain (range 0.3–4.1 kg). Time at sea ranged from 91 to 295 hours. Length of time at sea was not correlated with diving patterns or mass of the female (r^2 0.0). No correlation was found between mass of individuals and their diving patterns (r^2 0.0).

The mean maximum depth of dive for each deep diver was greater than 75 m whether considering day dives or night dives (Table 3). The mean maximum depth of dive for the shallow-diving females was less than 75 m (Table 3). When considering only night dives, shallow-diving females showed mean maximum depths of less than 50 m.

Two of the deep divers (195 and 651) showed no difference in depth of dives between day and night. The other seven females showed a significant difference in depth of dives between day and night. Six females dived deeper during the day than at night. The seventh (566) had significantly deeper dives at night than during the day (Table 3).

Time from shore to the first dive bout and return

The time between departure from shore and the first dive bout was highly variable, as was the time between the last dive bout and the return to shore (Table 2). These times ranged from about 3 to 34 hours. Mean time to first dive bout was 15.06 hours (SD 10.26) and the mean time from last dive bout to shore was 13.94 hours (SD 5.88). There was no significant difference between the time to first dive bout and the time from the last dive bout (Mann-Whitney $P = 0.86$).

There were no differences in either the time to the first dive bout or the time from the last dive bout when comparing shallow divers with deep divers. The mean time to the first dive bout was 12.30 hours (SD 8.74) for shallow divers and 18.51 hours (SD 12.26) for deep divers (Mann-Whitney $P = 0.46$). The mean time from the last dive bout to shore for shallow divers was 11.92 hours (SD 6.29) and for deep divers was 16.46 hours (SD 4.93; Mann-Whitney $P = 0.54$).

Foraging patterns

Deep divers showed a much lower percentage of dives at night than the shallow divers (Table 4). Females 566 and 695 made less than 50% of their dives at night. In general, shallow divers made greater than 70% of their dives at night (females 214 and 713 >90%) and deep divers less than 70%.

Table 3

Mean depth of dive for each dive record and for each record by day and night of nine female northern fur seals from St. Paul Island, Alaska, during July and August 1985.

	Record total			Day hours			Night hours			
Female ID	Mean depth	SD	*N*	Mean depth	SD	*N*	Mean depth	SD	*N*	*P*-value[1]
Deep divers										
195	101.5	22.0	440	102.1	18.3	205	101.0	24.8	235	0.590
566	75.3	31.2	439	72.4	28.0	285	80.8	35.9	154	0.007
651	76.0	27.3	496	75.3	27.0	193	76.5	27.4	303	0.632
695	85.1	34.1	504	93.0	30.8	259	76.7	35.3	245	0.001
Shallow divers										
214	38.7	23.1	1369	87.1	15.9	134	33.5	16.9	1235	0.001
308	60.6	42.1	832	94.8	41.6	230	47.5	34.3	602	0.001
713	45.4	21.7	900	85.1	25.4	55	42.8	18.7	845	0.001
767	33.3	27.7	431	72.9	22.6	90	22.8	17.6	341	0.001
854	40.6	28.2	312	63.6	15.2	80	32.6	27.3	232	0.001

[1]*P*-values are derived from a one-way ANOVA for differences in mean depth of dive between day and night hours.

Table 4

Total dives and dives/hour for day and night dives of nine female northern fur seals from St. Paul Island, Alaska, during July and August 1985.

		% total dives		Dives/hour		
Female ID	*N* dives	Day	Night	Total	Day	Night
Deep divers						
195	440	46.6	53.4	1.8	1.1	3.5
566	439	65.1	34.9	1.9	1.7	2.8
651	496	38.9	61.1	2.5	1.3	6.3
695	504	51.4	48.6	2.0	1.3	4.0
Shallow divers						
214	1369	9.8	90.2	4.7	0.6	16.8
308	832	27.6	72.4	3.4	1.3	10.0
713	900	6.1	93.9	5.0	0.4	20.1
767	431	20.9	79.1	3.8	1.0	14.6
854	312	25.6	74.4	3.4	1.2	9.7

The number of dives/hour for the entire trip was greater for shallow divers than for deep divers (Mann-Whitney, $P = 0.02$). The maximum number of dives/hour for deep divers was 2.5 ($\bar{x}$ 2.0, SD 0.31), whereas the minimum number of dives/hour for shallow divers was 3.4 ($\bar{x}$ 4.1, SD 0.75). Although deep divers tended to execute more dives per hour at night than during the day, the difference was not significant (Mann-Whitney, $P = 0.11$). Shallow divers did, however, make more dives per hour at night than during the day (Mann-Whitney, $P = 0.02$). Regardless of which diving pattern females exhibited, they always made more dives per hour at night than during the day.

Diving bouts

No differences in the total number of dive bouts per trip were detected between shallow and deep divers (Table 5). Although the number of dives that did not meet the dive-bout criteria tended to be greater for the deep divers, this difference was not significant (Mann-Whitney, $P = 0.07$). Differences in bout durations, number of dives per bout, and number of dives per hour within bouts were all greater for shallow divers (ANOVA, $P = 0.01$ for duration, $P = 0.01$ for dive number, $P = 0.02$ for dives/hour).

When all bouts were divided into those less than 75m and those greater than or equal to 75m, the percent of time spent below the surface was significantly different for shallow- and deep-diving bouts (ANOVA, $P = 0.01$). A greater percent of time was spent below the surface for shallow bouts (<75m, $\bar{x}$ 0.35 hour, SD 0.11, n 59) than for deep bouts (≥75m, $\bar{x}$ 0.29 hour, SD 0.12, n 102).

Pelagic fur seal studies

During the hours 0600–1000, the stomachs of 740 postpartum females were sampled, 504 over the shelf and 236 off the shelf (Table 6). From 1400 to 1900 hours, 750 postpartum females were sampled, 513 over the shelf and 237 off the shelf.

Females collected in the morning hours off the continental shelf were more likely to have food in their

Table 5

Dive bout[1] statistics and effort within dive bouts for nine female northern fur seals, from St. Paul Island, Alaska, in July and August 1985.

Female ID	Dive bouts	Dives excluded (%)	Bout duration (hours) $\bar{x}$	SD	Max.	Dives per bout $\bar{x}$	SD	Max.	Dives/hour in bout $\bar{x}$	SD	Max.
Deep divers											
195	26	4.8	2.5	2.3	9.2	16	13	51	8.9	5.7	28.0
566	24	10.5	2.8	2.0	7.9	16	13	54	6.6	4.2	16.7
651	15	4.4	3.8	3.0	11.7	32	26	93	8.4	4.0	16.2
695	26	9.3	2.7	1.8	7.7	18	14	63	7.0	4.2	17.8
Shallow divers											
214	20	3.0	3.8	2.2	8.3	66	65	163	13.5	10.3	32.3
308	25	4.9	3.0	1.8	7.7	32	37	135	10.5	10.0	35.7
713	9	1.8	4.6	2.4	8.2	98	75	184	20.1	12.8	33.3
767	7	3.2	4.2	2.9	7.8	60	55	145	12.8	6.7	24.4
854	9	2.6	3.0	1.9	8.6	34	24	74	13.2	9.5	30.3

[1] A dive bout is defined as any series of dives greater than five dives with surface intervals of less than 40 minutes (Gentry et al. 1986c).

Table 6

The percent of stomachs with food of lactating northern fur seals collected over the continental shelf (in water <200 m deep) and off the continental shelf (>200 m deep). Collections were made from July through September, 1958–74.

Time (hours)	Over the shelf	Off the shelf
0600–1000	80.0 (403/504)	95.3 (225/236)
1400–1900	54.0 (277/513)	39.7 (94/237)

stomachs than females collected over the shelf (chi-square, $P<0.001$). Afternoon samples showed a reverse trend with a higher incidence of food in stomachs of seals collected on the shelf than off the shelf (chi-square, $P<0.001$).

Discussion

Dive patterns and foraging locations

The results of this study show that northern fur seal females diving in deep water beyond the continental shelf primarily exhibit the shallow-diving pattern and dive predominantly at night. Females feeding at or near the shelf break may exhibit both diving patterns. Females located on the continental shelf (which had not already completed their feeding trip) were more likely to exhibit the deep-diving pattern and dived to depths of greater than 75 m throughout the day and night. However, females found over the continental shelf had, at times, shallow dive bouts (<30 m) at night.

The pelagic fur seal database provided insight into the relationship between diving patterns and feeding locations of fur seals in the Bering Sea. If the deep-diving pattern is associated with feeding on the continental shelf, and deep divers feed during the day, one can test the hypothesis that females found over the continental shelf during the day have a greater probability of having food in their stomachs than those females found off the shelf, which would be diving predominantly at night. The analyses of the northern fur seal pelagic database support our finding that the deep-diving pattern is associated with the continental shelf by showing that females collected over the continental shelf were more likely to be feeding during the day.

Dive patterns and probable prey

The feeding locations and dive patterns observed in this study are consistent with the known distribution of fur seal prey items. Kajimura (1984) summarized the variation in principal forage species for fur seals, depending on location. Fur seals feeding in the Bering Sea beyond the continental shelf over deep water fed on oceanic squid of the family Gonatidae (primarily *Gonatus* spp., *Berryteuthis magister*, and *Gonatopsis borealis*) or deep-sea smelts of the family Bathylagidae. These prey species, and fish with swim bladders, exhibit diel vertical migration and are at relatively shallow depths at night as they move vertically in synchrony with the deep scattering layer (Roper and Young 1975, Pearcy et al. 1977). It is during the night that they are fed upon by fur seals which rarely dive beyond 200 m (Gentry

et al. 1986b). Fur seals foraging over the shelf were likely to feed on walleye pollock *Theragra chalcogramma*, Pacific herring *Clupea harengus pallasi*, and capelin *Mallotus villosus* (Kajimura 1984). Each of these prey items is distributed throughout the water column over the shelf, depending on the sex and age of the individual and time of day; however, they are principally found near the bottom (Bakkala and Wakabayashi 1985). Even when prey are near the bottom over most of the shelf floor, they are shallower than the maximum diving depths observed for most fur seals and are accessible during all hours of the day.

The results of foraging effort for shallow and deep divers in this study are consistent with the results of Gentry et al. (1986c) in their study of diving of females from St. George Island. Costa and Gentry (1986) used isotopic turnover methods to measure food intake and metabolic rate in female fur seals instrumented with time-depth recorders. In that study of two deep-diving and two shallow-diving fur seals, the deep divers ate less food and expended less energy but gained similar body mass on a single trip to sea. Our results confirm their conclusion. In this study, using four measures—bout duration, dives per bout, dives per hour, and time spent below the surface—deep divers expended less effort on foraging than shallow divers. Deep divers apparently obtain greater energy per dive.

The difference in foraging effort of diving types may be explained by differences in energy content of prey, success rate for prey capture, and/or average size of prey captured. If success rate per dive and average size of prey were similar for both diving types, then energy content for the prey of deep divers would have to be greater. If prey were of similar size and energy content, then the prey of deep divers would have to be easier to capture. If success rate and energy content were similar, then the prey captured by deep divers would have to average a greater size per dive. Unfortunately, no data exist on success of individual dives.

Data on the energy content of prey items of northern fur seals suggest that Gonatus sp. and walleye pollock have similar energy content (M.A. Perez and T.R. Loughlin, NMFS Natl. Mar. Mammal Lab., Seattle, unpubl. data). No data exist for energy content of bathylagids. Perez and Bigg (1986) report on the size range of prey found in the stomachs of northern fur seals collected during 1958–74: walleye pollock, 4–40 cm (1721 prey from 71 stomachs); gonatid squid, 5–24 cm (>59 prey from 10 stomachs); deep-sea smelts, 8–12 cm (986 prey from six stomachs). The size range for Myctophiform fish prey and the mean size of prey were not reported.

Transit times

The most frequently used measure of transit time, derived from time-depth records, has been the time from shore to the first diving bout and from the last dive bout to shore (Gentry and Kooyman 1986). Data from the current study show that female fur seals frequently feed while traveling to very distant feeding locations and that the time from shore to the first diving bout is only a subset of the total time in transit.

There was no difference in the time from shore to the first dive bout for the two types of diving patterns observed in this study. Similarly, the times from the last dive bout to arrival ashore were not different. Furthermore, no correlation was found between these times and feeding trip duration. It has been suggested, however, that a correlation exists between feeding trip duration and distance to feeding area (Gentry et al. 1986a). Gentry et al. (1986a) found that regressing transit time of individuals upon their trip duration resulted in a poor fit (r^2 0.357). When they compared species averages using two tropical and two sub-polar otariid species, the correlation was much greater (r^2 0.761). They concluded that transit time may largely determine trip duration for the species, but its effect is partly obscured by the large variation in transit times and trip duration of some individual animals.

The results of Loughlin et al. (1987) and of this study show that females feed while in transit to primary foraging areas. A correlation may exist between trip duration and total time spent in transit; however, measuring the time from shore to the first diving bout and from the last diving bout to shore is only a subset of actual time spent in transit and therefore an inadequate measure of total transit time. Without knowledge of either the swim velocity or the location of females (either through radio-tracking or with some instrument carried by the animal to record location) it is not possible to discern from a record of a time-depth recorder the actual time spent in transit.

Classification of diving patterns

It is important to point out that any classification of diving patterns gives the impression that they are more discrete than they really are. It is more accurate to view any particular diving record as fitting into a continuum from strictly shallow diving at night to exclusively deep diving at all hours. The terminology used to categorize these diving patterns may overemphasize the importance of depth. It should be remembered that though deep- and shallow-divers are classified as such, the depth of dives may not be as important for identifying the pattern as the time of day in which diving occurs.

Before the advent of dive-recording instruments, one of the most important measurements used to assess changes in prey availability for pinnipeds and sea birds was the length of foraging trips. Foraging trips, however, may be useful only in documenting large-scale changes in prey availability (e.g., El Niño events). Dive-recorder instruments provide the opportunity to measure changes in the foraging environment on a finer scale. This work underscores the importance of quantifying dive patterns in elucidating differences in foraging strategies and in changes in the foraging environment.

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Potential Predation on Fish Eggs by the Lobate Ctenophore *Mnemiopsis leidyi* Within and Outside the Chesapeake Bay Plume*

John J. Govoni

Beaufort Laboratory, Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA, Beaufort, North Carolina 28516

John E. Olney

Virginia Institute of Marine Science, School of Marine Science
College of William and Mary, Gloucester Point, Virginia 23062

Abstract.– In Chesapeake Bay in June, the predatory lobate ctenophore *Mnemiopsis leidyi* and the eggs of the bay anchovy *Anchoa mitchilli* typically reach seasonal and localized abundance together. When examined at small vertical (1–3 m), horizontal (10–50 m), and temporal (6-hour) scales, the co-occurrence of *M. leidyi* and fish eggs (32.3–74.2% of which were *A. mitchilli*) was greatest in the northern reaches of the mouth of Chesapeake Bay, where the water column was well mixed, than in the southern reaches where the water column was stratified. Stratification to the south was effected by the Chesapeake Bay plume. With estimates of ctenophore clearance rate reported elsewhere and observed densities of ctenophores and fish eggs, potential predation was judged to be greatest in the northern reaches of the Bay mouth. The observation that co-occurrence and potential predation are greatest in areas where Chesapeake Bay water mixes with coastal shelf water implies that those fishes that spawn in low-salinity surface waters of well-stratified water columns may afford protection of their eggs from ctenophore predation.

Predation is probably the leading cause of mortality for fertilized fish eggs and yolksac larvae because starvation is not relevant for these early-life-history stages and because the short duration of egg incubation and yolk absorption for most teleosts limits transport to areas inimical to development (Bailey and Houde 1989). Assessments of the impact of predation on cohorts of fish eggs and larvae in the ocean, however, have been hindered by three problems: two practical, the third inferential. Eggs and larvae leave little identifiable residue in the guts of predators, and, as a result, direct estimates of the extent of predation are difficult. Predators and prey, moreover, are concentrated together in collecting devices, a situation that can result in artifically high feeding rates and inflated estimates of predation. Lastly, predation is often spuriously inferred from the inverse abundance of predators and prey, when presence and absence may actually reflect spatial and temporal segregation rather than removal of prey by predators. Such misinterpretations result from failure to consider the small-scale temporal and spatial distribution of predator and prey in differing water masses (Frank and Leggett 1982, 1985).

Among the known invertebrate predators of fish eggs and larvae, coelenterates and ctenophores are likely candidates for significant predation because of their high rates of ingestion and population growth (Alldredge 1984, Purcell 1985, Monteleone and Duguay 1988). Lobate ctenophores, in particular, are major predators of small zooplankton of limited mobility (Kremer 1979, Purcell 1985, Monteleone and Duguay 1988). They capture prey by pumping water past lobes lined with mucus and secondary tentacles (Larson 1988), a feeding mechanism that is seemingly well suited for the capture of fish eggs.

In Chesapeake Bay, a lobate ctenophore *Mnemiopsis leidyi* and the eggs of the bay anchovy *Anchoa mitchilli* reach seasonal and localized abundance together, thereby providing a predator and prey pair that is ideal for an evaluation of potential predation. *Mnemiopsis leidyi* is present from late fall through midsummer, and episodically explodes in abundance between May and July (Bishop 1967, Miller 1974, Kremer and Nixon 1976, Mountford 1980). *Mnemiopsis leidyi* can exhibit appreciable predation on fish eggs (*A.*

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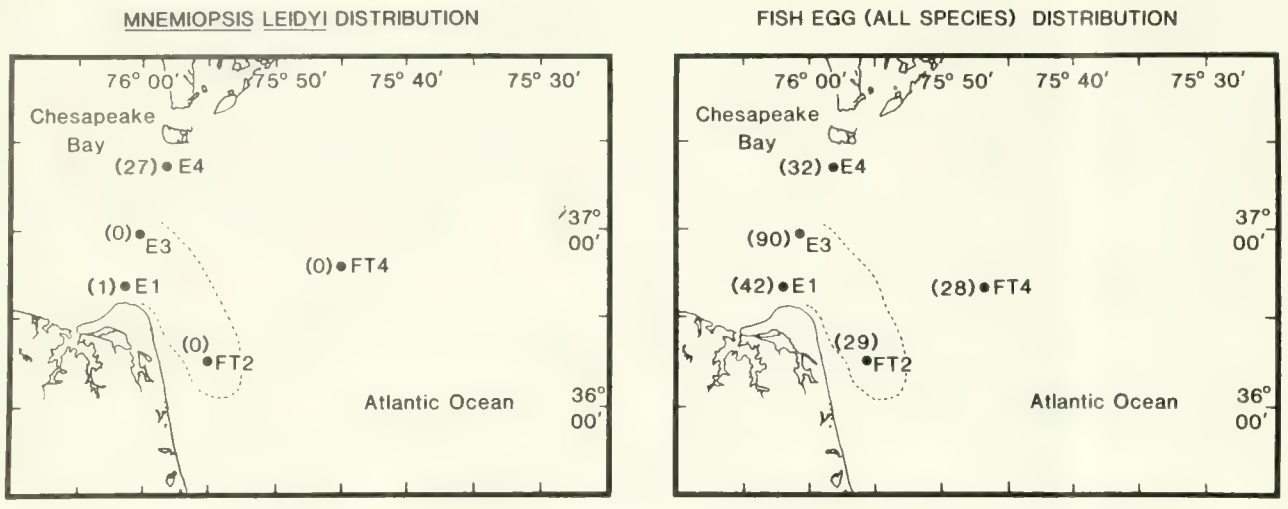

Figure 1

Positions of stations and mean station densities (numbers/m^3) of *Mnemiopsis leidyi* and fish eggs at the mouth of Chesapeake Bay. Dotted line indicates position of the Chesapeake Bay plume.

mitchilli) in the laboratory (Johnson 1987, Monteleone and Duguay 1988), but while it consumes some fish larvae in Chesapeake Bay (Burrell and Van Engel 1976), its predation on fish eggs in the field is not documented. *Anchoa mitchilli* spawns in the Bay in spring and summer and its eggs typically account for over 90% of all fish eggs present between May and August (Olney 1983).

The mouth of the Bay is characterized by water masses that differ spatially in both the vertical and horizontal dimensions (Boicourt et al. 1987) and provides hydrographic structure capable of shaping the spatial distribution of planktonic animals. Its complex hydrography is dominated by a buoyant plume characterized by a horizontal scale of 10–100 km, a vertical scale of 5–20 m, and a temporal scale of 1–10 days (Boicourt et al. 1987). As a result, the small-scale vertical and horizontal distributions of predator and prey can be observed synoptically in water columns of different structure within a confined study area.

Here we describe the small-scale spatial and temporal co-occurrence of *M. leidyi* and fish eggs at the mouth of Chesapeake Bay and assess potential predation.

Methods

Sampling protocol

Three stations were allocated across the mouth of Chesapeake Bay with two additional stations on the continental shelf (Fig. 1) such that some stations were within and others outside of the typical boundaries of the Chesapeake Bay plume (Boicourt et al. 1987). Each station was occupied for 30 hours between 11 and 21 June 1985 (the sampling period at station E1 was interrupted for 24 hours by vessel failure). At each station, hydrographic profiles (temperature, salinity, and specific gravity anomaly σ_t) and plankton collections at three nominal depths (surface, within the pycnocline, and below the pycnocline) were obtained once at four diel intervals (dawn, noon, dusk, and midnight). Fish eggs and ctenophores were collected with a 1-m Tucker trawl equipped with three 202-μm mesh nets, General Oceanic flow meters, and an Applied Microsystems Limited temperature, salinity, and depth recorder and towed at approximately 100 cm/second. Nets were opened at depth and fished along a horizontal trajectory for 30–60 seconds each; for subsurface strata, the trawl was lowered while the vessel was stopped and its nets were fished along a horizontal trajectory at depth. The trawl was positioned at nominal depth strata by the trigonometry of the warp angle and length. Triplicate samples were obtained at the surface; duplicate, discrete-depth samples were obtained within and below the pycnocline. With these sampling procedures, the trawl sampled on small vertical (1–3 m) and horizontal (10–50 m) scales.

All plankton collections were passed through a 6.4-mm mesh screen to separate ctenophores from ichthyoplankton. Ctenophores retained on this screen were fixed to prevent dissolution following the methods of Gosner (1971), then rinsed and preserved in 5%

formalin solution. Ichthyoplankton was preserved in either 5% formalin or 95% ethanol. All *M. leidyi* and fish eggs were counted except in those samples of exceptionally high ctenophore volume, where ctenophore number was estimated by volumetric subsampling and multiplication. Counts of ctenophores and fish eggs were averaged for replicate collections taken at a depth stratum and diel interval.

Estimation of co-occurrence

Our intention was to assess the small-scale co-occurrence of ctenophores and eggs relative to the water masses overlying these stations and to then evaluate potential predation. Because the depth of each sample occasionally varied from the nominal and the trawl consequently fished through hydrographic discontinuities, some collections were omitted from consideration. Collections omitted were those in which salinity values, recorded during each 30–60 second fishing interval, varied outside a range of 1.5‰. This procedure eliminated seven of 35 collections at station E1 and none at E4, the two stations where ctenophores and fish eggs were consistently present and where we focused our assessment of potential predation.

Estimates of potential predation

We estimated potential predation, for each depth and diel interval, as the product of clearance rate (the volume of water cleared of all prey per unit time per ctenophore), times the end points of the range of density of ctenophores (the number of ctenophores per unit volume, averaged for replicates), times the end points of the range in density of fish eggs (again averaged for replicates). A clearance rate of 168 L/day was used from Monteleone and Duguay (1988), who found that the clearance rate of fish eggs was independent of egg density (as well as the presence of alternate prey) and was positively and linearly related to experimental vessel size. This clearance rate was the highest rate observed for ctenophores 4.5–5.0 cm in length feeding in the largest vessels employed and falls roughly within the range of values reported elsewhere (Larson 1987). A sample of 10 preserved ctenophores from our collections averaged 8.5 mL in volume which converts to an average length of 4 cm (Kremer and Nixon 1976). We did not account for shrinkage.

Results

Distribution and co-occurrence

Mnemiopsi leidyi and fish eggs were consistently present only at stations E1 and E4 (Fig. 1). Pulses in densities of *M. leidyi* were evident, but did not conform to specific diel intervals or tidal phases (Figs. 2, 3). Egg density showed a diel pattern, with peak densities from dusk to dawn. Eggs of *Anchoa mitchilli* accounted for an average of 74.2% (range 23.0–98.5%) of the fish eggs at station E1 and 32.3% (range 0–62.9%) at E4.

Mnemiopsis leidyi and fish eggs were, for the most part, vertically segregated at station E1, but co-occurred, particularly in surface water, at E4. Vertical segregation at E1 (Fig. 2) reflected the physical stratification of the water column with a warm, low-salinity, surface-layer characteristic of the Chesapeake Bay plume overlying a cool, higher-salinity, bottom-layer characteristic of coastal shelf water (Boicourt et al. 1987). At E1, in the southern reaches of the mouth of the Bay, surface collections within the plume yielded higher egg densities, while subsurface collections yielded higher *M. leidyi* densities. Station E4, in the northern reaches and outside the plume, was unstratified with no thermo-, halo-, or pycnocline (Fig. 3). Water at this station apparently was a mixture of Chesapeake Bay water and coastal shelf water, likely the result of tidal, rather than wind, mixing. Winds, often responsible for mixing at the mouth of the Bay (Ruzecki 1981), were light to moderate during this sampling period (1–8 m/second).

Potential predation

Overall, potential predation was greater in the unstratified northern reaches of the mouth of the Bay outside the plume (E4) than in the southern reaches stratified by the plume (E1), because of greater temporal and spatial co-occurrence of *M. leidyi* and fish eggs there. Range estimates of potential population predation were 0.1–14.7 eggs per m^3/day at E1, and 0–174.3 at E4 (Table 1).

Discussion

The assessment of ichthyoplankton predation in the field has been based historically on the examination of predator gut contents or on the strength of a negative correlation of predator and prey densities, even though biases may result from the lability of fish eggs and larvae in the guts of predators, from the feeding of predators within the collecting device used to sample predator and prey (Purcell 1985), and from the spurious inference of cause and effect drawn from correlation analysis (Frank and Legget 1982, 1985). Few have resolved successfully the first two problems (Bailey and Houde 1989, Purcell 1989, Purcell and Grover 1990). In regard to the latter, the importance of small-scale spatial and temporal distribution of predator and prey

in evaluating predation is apparent across the mouth of Chesapeake Bay. Potential predation in the southern reaches where the Chesapeake Bay plume overlays coastal shelf water was low because of the relative lack of vertical co-occurrence there. In the northern reaches where the water column was well mixed, *M. leidyi* and fish eggs co-occurred in a more or less well-mixed water column, and as a result our estimates of potential predation were high.

The application of parameter estimates derived from laboratory predation experiments to the evaluation of the impact of gelatinous planktivores on their prey in nature, an approach that avoids field sampling errors, has other pitfalls (Purcell 1985). These problems relate to the unrealistic confines of experimental vessels, which constrain movement and small-scale hydrodynamics, and to unnaturally high experimental densities of predator and prey (Sullivan and Reeve 1982, de Lafontaine and Leggett 1988). The result is often artificially low estimates of clearance rate, values that are then used as functions in mathematical operations that range from simple multiplication of clearance rate and predator density (e.g., Reeve et al. 1978) to complex models that involve the swimming and foraging velocities and ambit geometries of motile predators and prey, and the turbulence of the environment in which they are embedded (e.g., Bailey and Batty 1983, Rothschild and Osborn 1988, Evans 1989). The simple approximation used herein was justified, in part, by the behavior of *M. leidyi* feeding on immobile fish eggs. Lobate ctenophores feed as a moving pump, pumping water continuously through mucus- and tentacle-lined lobes, while either swimming vertically or hovering (Larson 1988), and changing position in response to low prey density (Reeve et al. 1978). While the geometry of the predatory field of *M. leidyi* is unknown, we assume, given forage velocities of from 1–3 mm/second for its congener *M. mccradyi* (Larson 1987), that it encounters new water continuously. Although the gut capacity of lobate ctenophores is small, *M. leidyi* egests superfluous food in a mucus bolus when its gut is full and continues feeding; egested fish eggs, embedded in this bolus, are either dead or moribund (Johnson 1987).

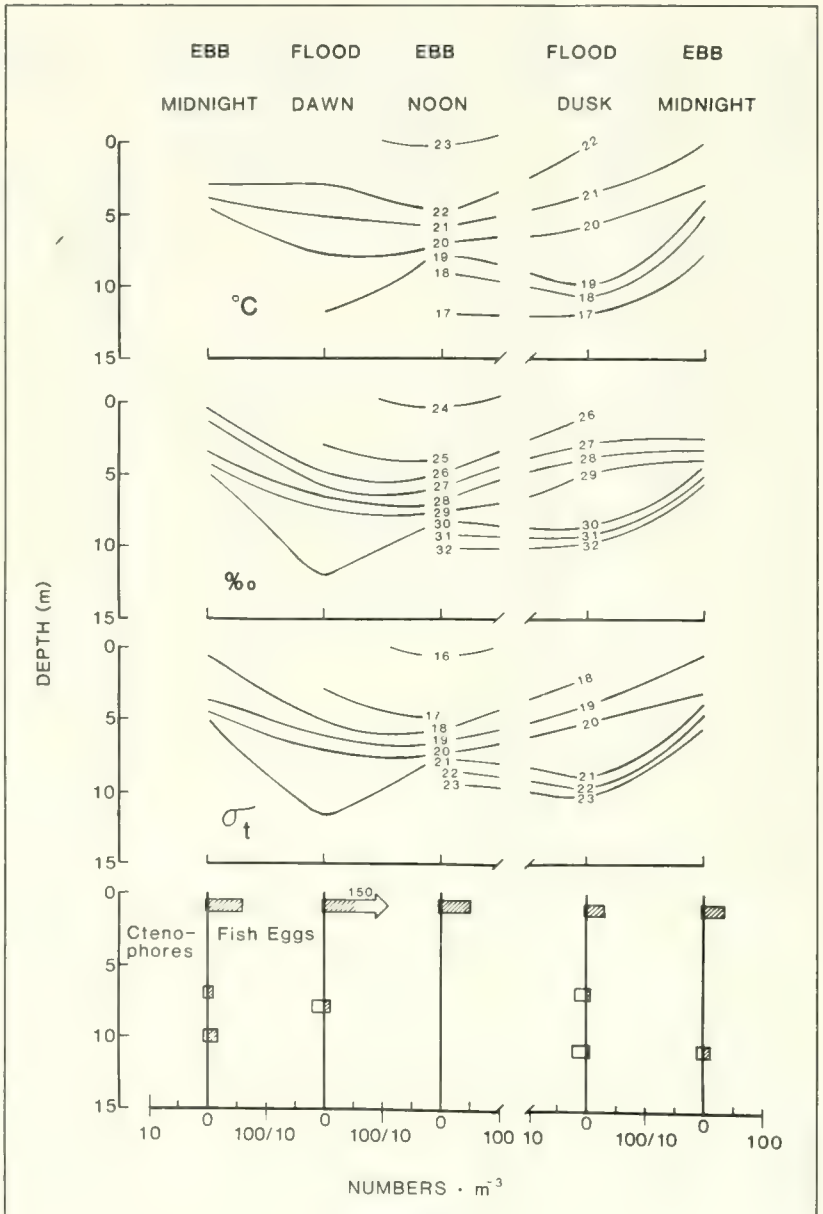

Figure 2

Temporal hydrographic sections (temperature, salinity, sigma-t) and densities (numbers/m^3) of *Mnemiopsis leidyi* and fish eggs at station E1 at the mouth of Chesapeake Bay. Vessel failure caused a 24-hour interruption in sampling between noon and dusk.

The observation that co-occurrence of *M. leidyi* and fish eggs, and consequently potential predation, is greatest in areas where Chesapeake Bay water mixes with coastal shelf water, coupled with the observation that *M. leidyi* are more abundant in regions of higher salinity within other estuaries, implies that those fishes

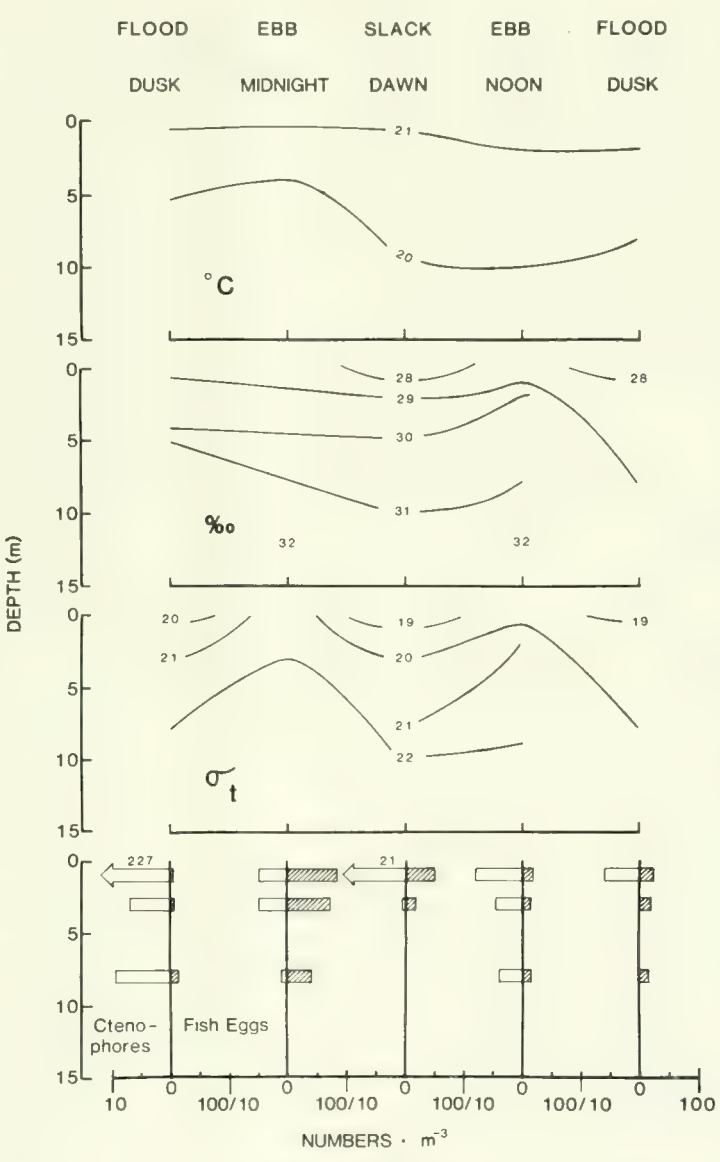

Figure 3

Temporal hydrographic sections (temperature, salinity, sigma-t) and densities (numbers/m^3) of *Mnemiopsis leidyi* and fish eggs at station E4 at the mouth of Chesapeake Bay.

Table 1

Potential predation of the lobate ctenophore *Mnemiopsis leidyi* on fish eggs at the mouth of Chesapeake Bay. Values are the end points of the range over five diel intervals.

	Potential predation rate (eggs/m^3 × day)	
Strata	Station E1	Station E4
Surface	0.1–14.7	21.0–174.3
Pycnocline	1.6–4.4	0–68.8
Below pycnocline	0.5–3.8	0–25.1

that spawn in low-salinity surface waters of well-stratified water columns may afford protection of their eggs from ctenophore predation. Estuaries typically fluctuate between stratified and unstratified conditions as a result of lunar periodicity and meteorological forcing. A survival advantage may be afforded by spawning in association with the predator free surface waters of the Chesapeake Bay plume.

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Abstract.–Spring ichthyoplankton surveys in the tidal freshwater reaches of Virginia rivers were used to document the temporal and spatial occurrence of spawning by striped bass *Morone saxatilis* (Walbaum). Single river systems were intensively surveyed in 1980 (York River system), 1981 (James River system), and 1982 (Rappahannock River). In spring 1983, all three river systems were sampled at approximately weekly intervals. Some spawning occurred in all years, including those yielding poor year-classes (1980 and 1981). Spawning occurred largely within the first 40 km of tidal freshwater in major rivers, except when drought conditions displaced spawning upstream in advance of encroaching saltwater. Eggs appeared in sharp, brief peaks of abundance, usually between the third week in April and the first week in May. Peak densities coincided with rapidly rising water temperatures in the range 13.7–19.5°C.

Distribution of Striped Bass *Morone saxatilis* (Walbaum) Eggs and Larvae in Major Virginia Rivers*

George C. Grant
John E. Olney

Virginia Institute of Marine Science, School of Marine Science
College of William and Mary, Gloucester Point, Virginia 23062

The importance of Chesapeake Bay spawning grounds to Atlantic coast stocks of striped bass *Morone saxatilis* (Walbaum) has long been recognized (Merriman 1941; Raney 1952; Briggs 1962; Alperin 1966; Schaefer 1967, 1968, 1972; Berggren and Lieberman 1978; Kohlenstein 1981; Fabrizio 1987a, 1987b). Striped bass spawning in Chesapeake Bay and its tributaries has been documented from collections of eggs and larvae (Tresselt 1952, Rinaldo 1971, Johnson and Koo 1975, Polgar et al. 1976, Conte et al. 1979, Kernehan et al. 1981, Setzler-Hamilton et al. 1981), and survey data on the distribution of juveniles or presence of ripe adults (Vladykov and Wallace 1952, Grant and Joseph 1969, Markle and Grant 1970, Grant 1974).

Direct documentation of striped bass spawning in Virginia rivers based on plankton collections of eggs and larvae was provided by consecutive single surveys of five rivers in April and May 1950 (Tresselt 1952); a single river survey during the entire 1966 spawning season (Rinaldo 1971); and a single river survey during the entire 1985 spawning season (McGovern and Olney 1988). This paper documents temporal and spatial occurrence of striped bass eggs and larvae in Virginia's major river systems. The York, James, and Rappahannock river systems, respectively, were surveyed in the years 1980–82; all three rivers were sampled in 1983.

Methods and materials

Lower tidal freshwater portions of the James, Chickahominy, Pamunkey, Mattaponi, and Rappahannock Rivers were divided into 3-mile (5-km) strata, from which single stations were randomly selected prior to each sampling trip. Number of strata (in parentheses) and cruise dates were: the Pamunkey River (10), 16 April–13 June 1980 and 5 April–11 May 1983; Mattaponi River (6), 18 April–14 June 1980; James River (10), 22 April–19 June 1981 and 8 April–8 May 1983; Chickahominy River (7), 21 April–18 June 1981; and Rappahannock River (9), 5 April–6 June 1982 and 9 April–13 May 1983.

Stations were sampled semi-weekly to weekly within strata extending upstream from the limits of brackish water (~0.5‰) to beyond the observed occurrence of striped bass eggs. Collections at each station were stepped-oblique, daylight tows of a 60-cm bongo sampler, equipped with 333-μm mesh nets and flowmeters. Length of tows were 2–6 minutes; tows in deep water were of longer duration and tows encountering excessive detritus loads were shortened. Catches from the paired nets

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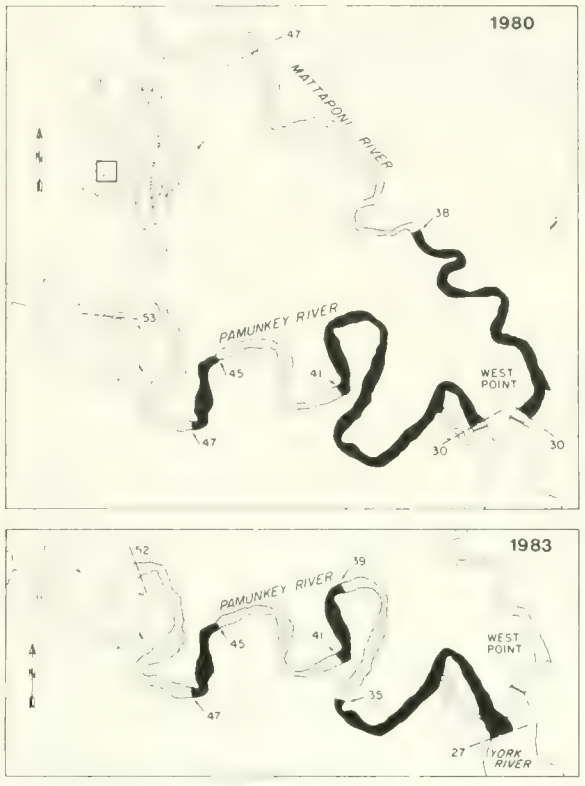

Figure 1
Spatial extent of observed striped bass egg occurrence, Pamunkey and Mattaponi rivers, 1980 and 1983. Over 80% of eggs occurred in solid black areas. Inset shows location in Chesapeake Bay region.

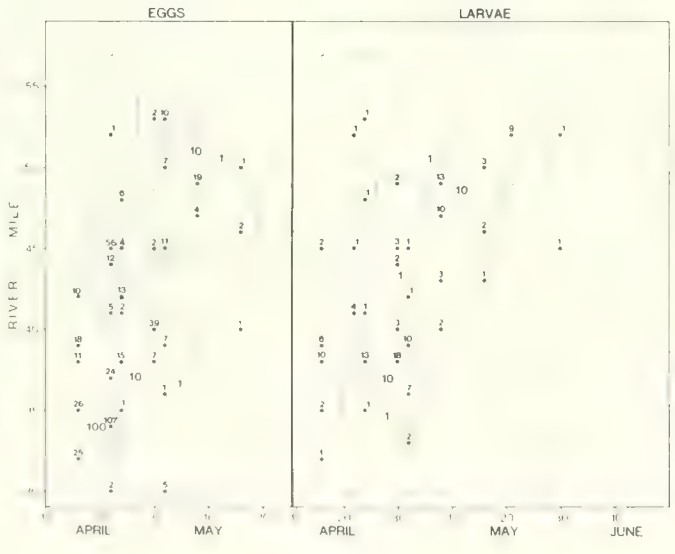

Figure 2
Spatial and temporal abundance (numbers/100 m^3) of striped bass eggs and larvae in the Pamunkey River, 1980. River miles are nautical miles above the York River mouth.

were combined and preserved in 5–8% buffered formalin. Sampling in 1983 was intended to document only egg occurrence; however, surveys on 4 and 11 May 1983 yielded some larval data. Surface and bottom measurements of temperature, salinity, and dissolved oxygen were made at each station.

Whole collections were sorted for striped bass eggs and *Morone* spp. larvae, except where large amounts of detritus necessitated examining only one-half of the collection. When bits and pieces of striped bass eggs were found, only intact eggs and separated embryos were counted. The area of peak spawning was defined as those strata that cumulatively contributed >80% of all eggs collected. *Morone* larvae lacking yolk material and larger than 8.5 mm standard length were cleared and stained for positive identification (Fritzsche and Johnson 1980, Olney et al. 1983).

Results

York River System, 1980 and 1983

Spawning extended approximately 40 km upstream from the limit of brackish water in the Pamunkey River in 1980 and 1983 and 27 km in the Mattaponi River in 1980. Peak spawning was recorded over 13 km on the Mattaponi River, while on the Pamunkey River it was observed in two disjunct regions (miles 27–41 and 45–47) in both years (Fig. 1). In 1980, eggs were found on initial surveys (April 16 and 18), indicating that spawning activity had already begun (Figs. 2, 3). Peak egg densities (>1/m^3) occurred on 22 and 25 April in the Pamunkey and Mattaponi rivers, respectively. In 1983 (Fig. 4), sampling on the Pamunkey River was initiated on 5 April, but few eggs were collected until 27 April, when peak densities for the season were encountered.

Abundance of larval striped bass was centered somewhat further upstream than eggs on the initial 1980 surveys, and all were yolk-sac larvae. Peaks in egg and larval abundance coincided more closely on subsequent sampling dates (Figs. 2, 3). Few larvae were collected after the 8 and 9 May surveys of the Pamunkey and Mattaponi rivers, none after 31 May.

Modal length of larvae in both rivers was 5 mm NL (notochord length) and most were yolksac larvae. All larvae captured after 16 May were 12 mm SL (standard length) or larger. In 1983, all larvae from the surveys of 4 and 11 May (the only collections examined for larvae) were yolksac larvae less than 6 mm in length.

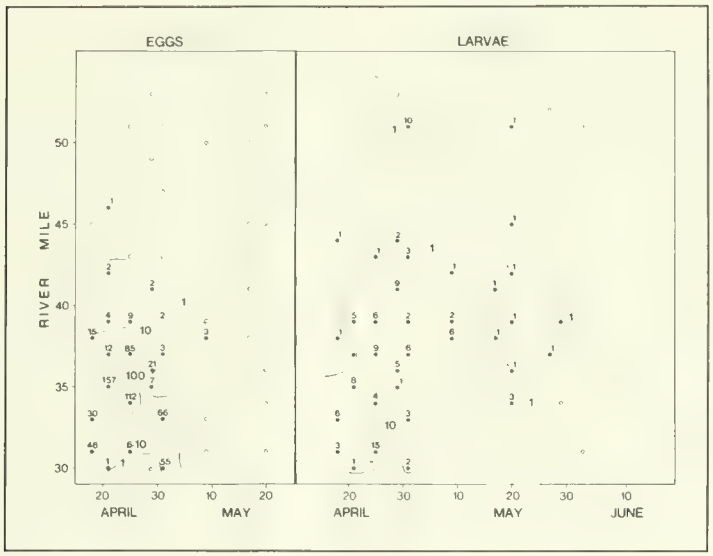

Figure 3
Spatial and temporal abundance (numbers/100 m^3) of striped bass eggs and larvae in the Mattaponi River, 1980. River miles are nautical miles above the York River mouth.

James River System, 1981 and 1983

Location of peak spawning and maximum densities of eggs differed considerably between 1981 and 1983 (Fig. 5). Occurrence of eggs much farther upstream in 1981 was probably related to drought and intrusion of saltwater in winter and spring, 1980–81. Spawning extended over 35 km in 1981, and over 40 km in 1983. In both years

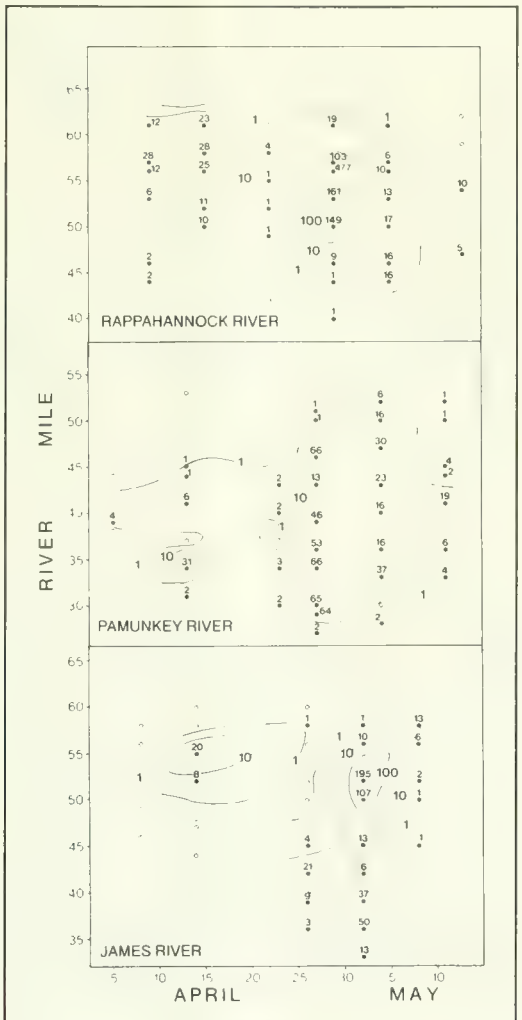

Figure 4
Spatial and temporal abundance (numbers/100 m^3) of striped bass eggs in three Virginia rivers, 1983. River miles are nautical miles.

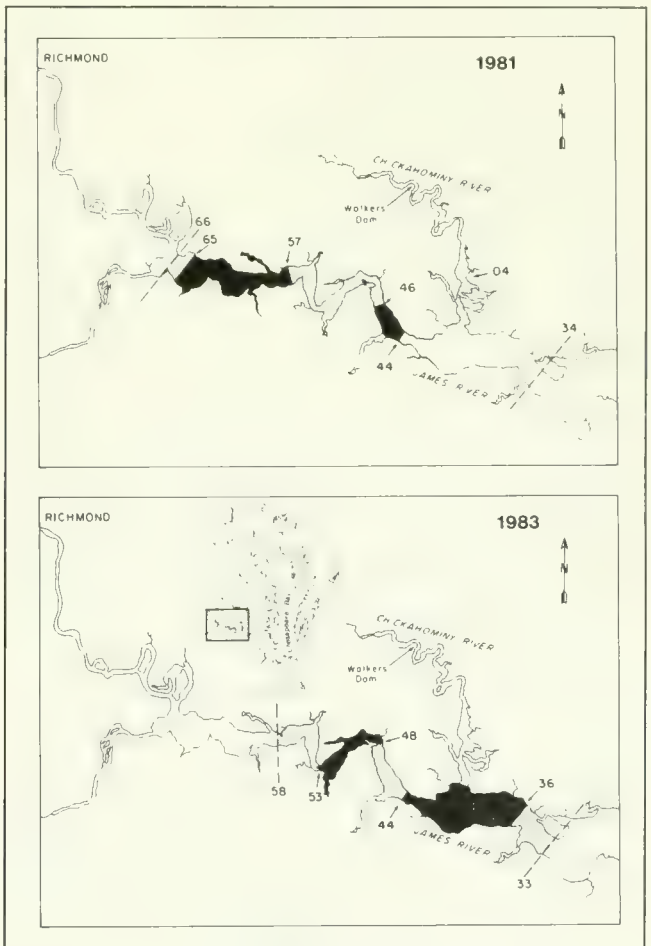

Figure 5
Spatial extent of observed striped bass egg occurrence, James River, 1981 and 1983. Over 80% of eggs occurred in solid black areas. Inset shows location in Chesapeake Bay region.

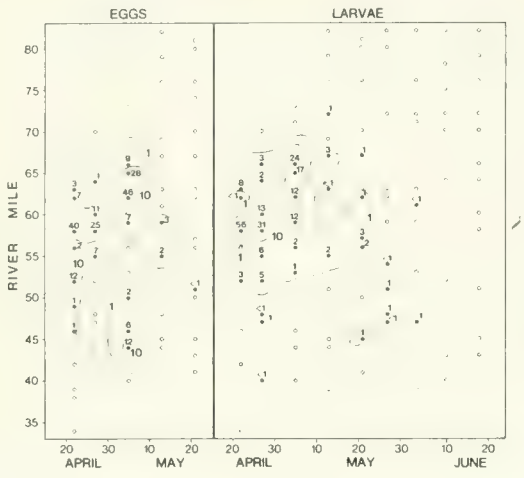

Figure 6

Spatial and temporal abundance (numbers/100 m^3) of striped bass eggs and larvae in the James River, 1981. River miles are nautical miles above the river mouth.

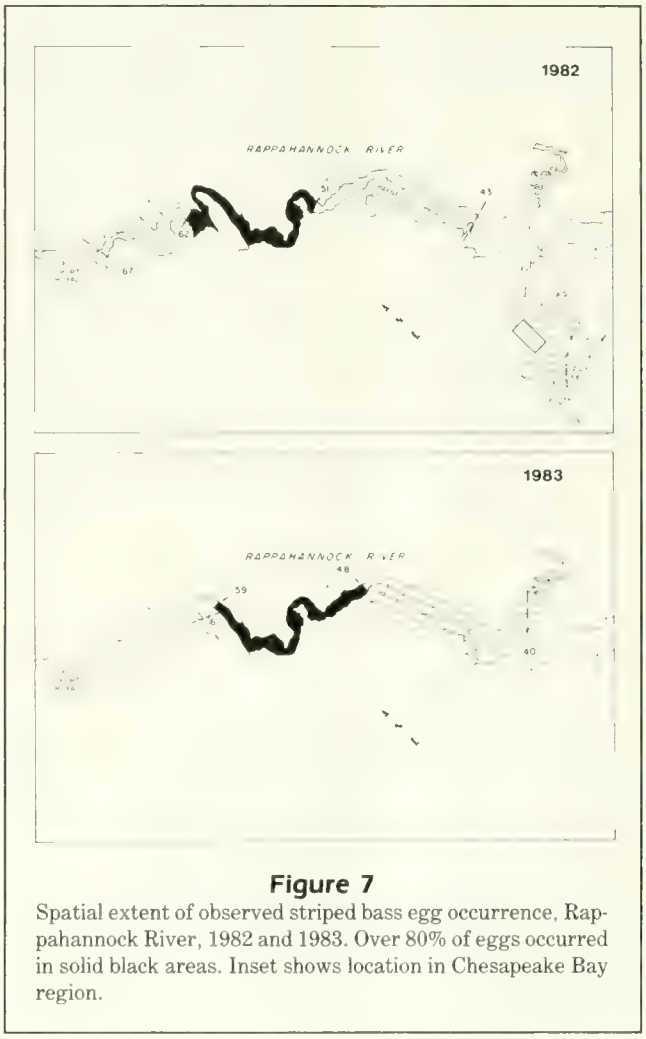

Figure 7

Spatial extent of observed striped bass egg occurrence, Rappahannock River, 1982 and 1983. Over 80% of eggs occurred in solid black areas. Inset shows location in Chesapeake Bay region.

peak spawning appeared to be bimodally distributed along the river channel. Eggs were present in both rivers on initial surveys of 1981 (21 April in the Chickahominy River and 22 April in the James River) in fresh to slightly brackish water and temperatures of 15.6–18.7°C. Maximum egg densities in the James River were only 46/100 m^3 in 1981 (13/100 m^3 in the Chickahominy), compared with 195/100 m^3 in 1983. These maxima occurred in both years during the first week in May, in tidal freshwater and similar temperatures (18.5–19.5°C), but at sites separated by 16 km (Fig. 6). In the Chickahominy River, eggs were restricted to the river's junction with the James and found on only two surveys, suggesting that eggs could have been spawned in the James River and tidally advected into the Chickahominy.

Larval striped bass were not present in collections from the Chickahominy River in 1981, and the river was not sampled in 1983. James River collections in 1981 yielded primarily yolksac larvae, found in maximum densities similar to those of eggs (Fig. 6). The modal length of larvae during the first 3 weeks of surveys in 1981 was 5.0–5.9 mm, but a few smaller larvae (4.0–4.9 mm) were hatched as late as 21–22 May. The maximum size of larvae increased from 7.0–7.9 mm in late April to over 13 mm on 4–5 June, the last survey in which striped bass larvae were captured. Only a dozen larvae larger than 9 mm were collected. In 1983, larvae from the early-May surveys attained densities of 31/100 m^3.

Rappahannock River, 1982 and 1983

Eggs were found within the first 40 km of tidal freshwater in both 1982 and 1983 (Fig. 7). Peak spawning was observed between river miles 51 and 62 in 1982 and miles 48 and 59 in 1983. Eggs occurred in densities ranging between 1.4–330/100 m^3 during April 1982 and 0.7–50/100 m^3 in May of that year. None were found after the 11 May survey, and the maximum density occurred on 21 April in temperatures 15.7–16.6°C. In 1983, eggs were collected in all weekly surveys from 9 April to 13 May, but increasing densities were reversed by a cold snap in the third week of April, when only scattered eggs were found (water temperatures had declined from 13–14°C to 11–12°C). Egg densities peaked once water temperature rose in the last week of April, when a maximum of 477 eggs/100 m^3 was recorded. Eggs were rare by the final sampling date (May 13).

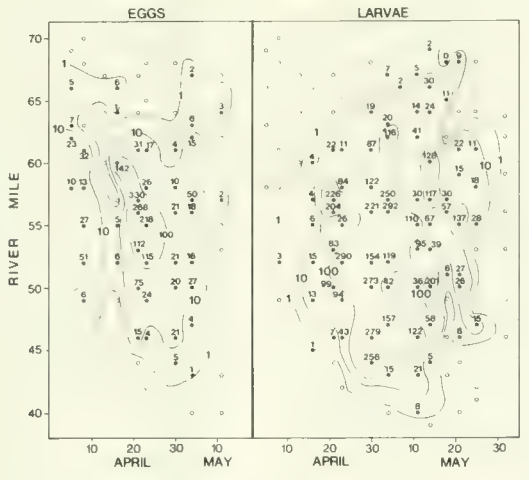

Figure 8

Spatial and temporal abundance (numbers/100 m^3) of striped bass eggs and larvae in the Rappahannock River, 1982. River miles are nautical miles above the river mouth.

Peak larval densities were recorded on the Rappahannock River in 1982 during late April and early May (Fig. 8). These densities were the highest observed in our 3-year study of Virginia rivers. Modal lengths of larvae were 5–6 mm NL until mid-May; all larvae from 21 May to the conclusion of sampling in June were at least 8 mm in length. In 1983, larvae from the early May surveys were all less than 8 mm in length and attained a maximum density of 103 larvae/100 m^3.

Discussion

Tresselt (1952), Rinaldo (1971), McGovern and Olney (1988), and this study constitute the only direct observations on striped bass eggs and larvae in major Virginia rivers. Striped bass spawning in Virginia rivers occurred from early April through the first week or two in May 1980–83, and within the first 40 km of tidal freshwater, generally confirming earlier observations of Tresselt (1952) and Rinaldo (1971).

Tresselt (1952) observed spawning on the two major rivers of the York River system, the Pamunkey River (4–13 April 1950) and the Mattaponi River (13–30 April 1950). He found largest numbers of eggs 27 km above the mouth of the Pamunkey and 14 km above the mouth of the Mattaponi. Historic centers of successful spring fishing for striped bass were in these tidal freshwater rivers. Spawning in the Pamunkey River in 1966 occurred 8–48 km above West Point during 24 April–13 May 1966 (Rinaldo 1971). Surveys of Virginia striped bass spawning grounds in 1950 (Tresselt 1952) were inadvertently somewhat late in the Chickahominy and James rivers, but provide the only direct documentation of striped bass spawning prior to the present study. He found only three eggs in 30 collections in the Chickahominy River, 5–8 May 1950, and 57 eggs in 38 collections from the James River during 9–10 May. No direct observations on striped bass larvae were made prior to the present study. Use of the Rappahannock River as a spawning site by striped bass was also documented by Tresselt (1952), although his limited survey (four sampling dates in May 1950) yielded only five eggs.

Temporal occurrence of striped bass spawning is similar throughout Chesapeake Bay. In Virginia rivers, peaks in spawning were sharp and of limited duration. They occurred in the fourth week of April in York River tributaries in both surveyed years (1980 and 1983) and in the Rappahannock River in 1983; peak spawning was a week earlier in the Rappahannock River in 1982. Spawning in the James River was somewhat later, peaking in the first week of May in both 1981 and 1983. Peak spawning in this time-period is also typical for the Potomac River (Setzler-Hamilton et al. 1981) and in the upper Chesapeake Bay and Chesapeake and Delaware Canal (Johnson and Koo 1975, Kernehan et al. 1981). Although striped bass eggs were found in a wide range of temperatures (8.0–21.2°C), peak densities were limited to rapidly rising temperatures in the range 13.7–19.5°C and nearly always to freshwater. Annual differences in time of spawning within a given river system are most likely a result of differences in temperature and the rate of vernal warming.

Areas of peak spawning and the spatial extent of the spawn are remarkably similar among years and river systems, but differences can occur in years of drought. The present data from the James River contrasted a year of severe drought (1981) with one of near-average rainfall (1983). The estimated streamflow from the James River system into Chesapeake Bay during March, April, and May averaged only 69,000 cfs in 1981 compared with 180,000 cfs in 1983 (monthly summary reports of estimated streamflows entering Chesapeake Bay, 12/30/81 and 12/30/83, U.S. Geol. Surv., Towson, MD). Peak egg production was displaced 15 km upriver in 1981, in advance of encroaching saltwater, whereas interannual differences in location of peak spawning in the other river systems where drought was not a factor were insignificant (<2 km).

The tidal freshwaters of the Rappahannock River were surveyed for striped bass eggs and larvae in the spring of 1982, during production of what later was determined to be the strongest year-class measured in Virginia during the period 1971–82 (Colvocoresses

1989). The observed high density of eggs and larvae in 1982 and subsequent success of the 1982 year-class support the concept that attributes strong year-classes to exceptional survival of eggs and larvae on the spawning grounds, rather than absolute size of spawning stock (management actions designed to prevent overfishing and to increase size of spawning stock were not yet in effect). After 10 years of poor year-classes, i.e., 1972–81, the stock producing this 1982 year-class must necessarily have been small. Chapman's (1987, 1989, 1990) discovery of differences between genotype frequencies of 1982 year-class males and those of older Chesapeake Bay females is more direct evidence that strong year-classes can stem from successful spawning by relatively few females. Unfortunately, we have yet to determine which factors govern survival and growth of striped bass eggs and larvae on Chesapeake Bay spawning grounds, although recent research efforts are addressing this important question (e.g., McGovern and Olney 1988, Chesney 1989, Uphoff 1989).

Acknowledgments

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Growth, Mortality, and Movements of Juvenile California Halibut *Paralichthys californicus* in Shallow Coastal and Bay Habitats of San Diego County, California

Sharon Hendrix Kramer

Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA
P O Box 271, La Jolla, California 92038
Present address: MBC Applied Environmental Sciences
947 Newhall Street, Costa Mesa, California 92627

Abstract.– Growth and mortality rates were compared for juvenile California halibut *Paralichthys californicus* from bay and open coast habitats. Growth was estimated by determination of size-at-age using daily increments in otoliths. No significant difference was observed in size-at-age for juvenile halibut between 6 and 41 mm from the bays and open coast. However, age-specific mortality rates estimated for halibut <70 days were highest for newly-settled halibut on the open coast. California halibut settled either in bays or on the open coast, but ultimately nearly all of the halibut that settled on the coast entered and used the bays as nursery areas during their first year of life or else they died. The advantages of bays as nursery areas may be a decrease in risk of mortality of newly-settled halibut and an increase in growth of larger juveniles that feed upon the abundant small fishes in the bays.

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The utilization of specialized nursery habitats by juvenile fish is a common phenomenon (Boehlert and Mundy 1988, Miller et al. 1986). Many of the fish species that utilize bays as nursery areas spawn in offshore waters, and move into bays as late larvae and early juveniles (Boehlert and Mundy 1988, Miller et al. 1986). The migration, location, and entry of larvae and juveniles into the bays involve complex behaviors that are particularly important on the Pacific coast of North America, where only 10–20% of the coastal habitat consists of estuaries and lagoons, compared with 80–90% on the Atlantic and Gulf coasts (Emery 1967). Possible consequences of the use of bays as nursery areas include faster growth because of high food production, warm temperatures, and decreased predation (Miller et al. 1986, Kneib 1987, Krygier and Pearcy 1986).

The California halibut *Paralichthys californicus* is a commercially important flatfish found in southern California coastal waters and bays (Frey 1971, Haaker 1975, Allen 1988, Love et al. 1986, Plummer et al. 1983). Eggs and larvae occur over the shelf and seaward, with greatest densities in waters less than 75 m deep and within 6 km of shore (Frey 1971, Gruber et al. 1982, Barnett et al. 1984, Lavenberg et al. 1986, Walker et al. 1987, Moser and Watson 1990). In past studies juvenile halibut rarely were taken on the open coast, suggesting that bays and lagoons might be the only significant nursery habitat (Plummer et al. 1983, Allen 1982, Kramer 1990).

The objective of this study was to determine the relative importance of bays as nursery areas and to evaluate the movements between bay and open coast habitats. To meet these objectives, I estimated habitat-specific distribution, abundance, and growth and mortality rates of juvenile halibut from both bay and open coast habitats.

Materials and methods

Distribution and abundance

California halibut were collected during a 2-year survey (September 1986–September 1988) of the open coast between Mission Bay and San Onofre, and two bays, Mission Bay and Agua Hedionda Lagoon (Fig. 1). A stratified random sampling design was used, consisting of four open coast blocks each with three depth strata (5–8 m, 9–11 m, and 12–14 m), and five blocks in Mission Bay and three blocks in Agua Hedionda Lagoon, each with three depth strata (0–1 m, 1–2 m, and 2–4 m) (Fig. 1).

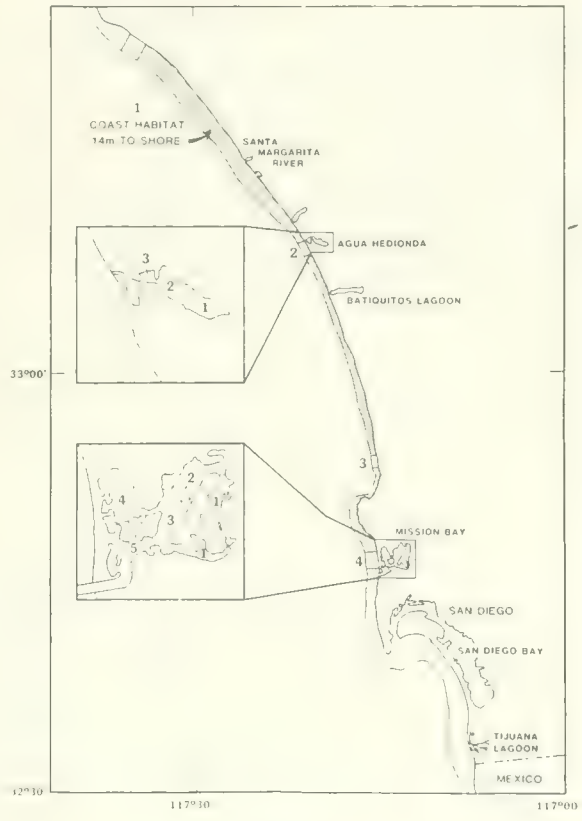

Figure 1

Location of sampling blocks. Open coast blocks are (1) San Onofre, (2) adjacent to Agua Hedionda Lagoon, (3) Torrey Pines, and (4) adjacent to Mission Bay. The two bays sampled are Agua Hedionda Lagoon and Mission Bay, with sampling blocks denoted.

For further description of the sampling design and the habitats see Kramer (1990).

Three gear types were used, all lined or made of 3-mm mesh: a 1.0-m wide beam trawl, a 1.6-m wide beam trawl, and a 1×6-m beach seine. The 1.6-m beam trawl, set from a 15-m research vessel, was used to sample the open coast and Mission Bay (Fig. 1). I sampled Agua Hedionda Lagoon and the areas of Mission Bay that were inaccessible to the larger vessel with the 1.0-m beam trawl, set from a 6-m skiff. The 1.0-m beam trawl and the beach seine were pulled along the bottom by two people to sample the shallow shoreline (<1 m) in the bays. The trawls were fitted with a wheel and revolution counter to determine the distance traveled by the trawl along the bottom, allowing a quantitative assessment of fish density since the trawls had a fixed mouth opening (Krygier and Horton 1975). All trawls and seines were fished during the day.

Table 1

Gear weighting coefficients and their variances by length-class for conversion of shoreline collections by beach seine and 1-m beam trawl. Coefficients determined by 3-way ANOVA between gear types, blocks, and months of sample on density for each length-class. Correction terms are given for length-classes with significant gear effects ($P \leq 0.05$). There were no significant gear effects in the 1.0–1.6 m beam trawls for open water tows.

Length class (SL, mm)	Correction term	Variance
26–30	3.291	0.124
31–35	4.398	0.319
36–40	2.752	0.099
41–45	4.699	0.359

All flatfishes taken in trawls and seines were measured to standard length (SL) in mm. Density of halibut in 5-mm standard length-classes was determined for juveniles ≤70 mm SL. The thirteen length-classes used were: SL≤10 mm, 11–15 mm, 16–20 mm, continuing to 66–70 mm SL. Abundance was determined by multiplying the mean density for each habitat by the area of each habitat.

Gear comparison

Densities based on the 1.0-m beam trawl collections did not differ significantly from those of the 1.6-m beam trawl for any length class (ANOVA, $P>0.05$, n 826). However, the beach seine captured significantly fewer small halibut (26–45 mm SL) than the 1.0-m beam trawl (Table 1). Since significant biases existed, density and abundance estimates of halibut were corrected for the differences in gear efficiency by weighting the mean density and variance for each length class where significant differences in catchability were found (Table 1).

The weighted mean density for each gear type was calculated as

$$d_w = (d_1 + gd_2)/(1 + g)$$

where d_1 = unweighted density, d_2 = weighted density, and g = weighting coefficient.

Estimated variance of the weighted mean d_w was calculated as

$$V(d_w) = V(d_1) + g^2V(d_2) + d_2^2V(g) + V(g)V(d_2)$$

where $V(d_1)$ = variance of unweighted density, $V(d_2)$ = variance of weighted density, and $V(g)$ = variance of

weighting coefficient. Variance of the weighted mean was underestimated because the covariance terms were not included. Resampling techniques to estimate variance (e.g., bootstrap) were impractical because of the large size of the database.

Age validation and determination

Laboratory-reared halibut larvae of known age were measured to standard length in mm and their sagittae excised and mounted in resin (Eukitt, O. Kindler, West Germany) on a microscope slide. Age was estimated using the methods of Methot (1981) and Butler (1987). A microcomputer interfaced to an electronic digitizer was used to measure and count increments on a projected image of the otolith from a high-resolution video camera mounted on a compound microscope. Increment counts of 45 larvae (3.1–9.1 mm SL) that were reared at 16–20°C in the laboratory were regressed against the known age of the larvae to establish a relationship between estimated and known age. Increments were formed daily: the slope of the relationship (0.969) did not differ significantly from unity ($P>0.05$). The regression of the number of increments on age of halibut larvae (5–29 days) was

$$\text{Age (days)} = 3.496 + 0.969 \times \text{(no. increments)}$$

where $r^2 = 0.981$, SE constant = 1.055, SE slope = 0.018, and range of increment counts = 1–26) (Fig. 2). Daily formation of rings has also been found in juveniles 30–70 mm SL (Kicklighter 1990). The first increment is deposited about 3.5 days after hatching, coinciding with the day of first feeding (Gadomski and Peterson 1988). I added 3.5 to the number of increments counted on the otolith so that age was equivalent to the number of days from hatching.

Ageing of field-caught halibut

Juvenile halibut from field collections were measured alive and either frozen or preserved in 80% ethanol. Sagittae were dissected and increments counted using the techniques described above. Sagittae from juveniles >20 mm SL were polished with 400- and 600-grit wet sandpaper before counting.

A total of 120 field-caught halibut were aged: 50 from Mission Bay, 19 from Agua Hedionda Lagoon, and 51 from the open coast. Larval sagittae are symmetrical and nearly circular (Fig. 3A), but after metamorphosis additional foci develop and the sagittae became asymmetrical, with maxiumum deposition along the rostral axis (Karakiri et al. 1989) (Fig. 3B). This shift in the axis of sagittal growth produces areas

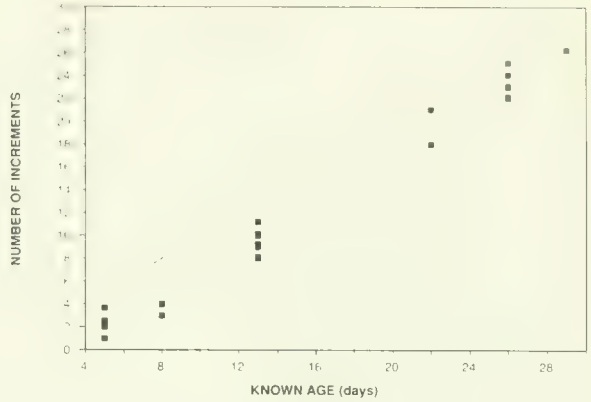

Figure 2
Age validation of California halibut sagittae. Number of increments counted on the sagittae are compared with the known age of laboratory-reared larval halibut (n 45). Straight line represents a one-to-one relationship of increment number and known age.

that are difficult to interpret (Fig. 3). These areas correspond to a period of about 7 days after metamorphosis. I estimated the number of increments in regions of transition between foci by counting the number of increments that occurred in an adjacent area on a different axis (Fig. 3). The relationship between standard length (mm) and otolith radius (μm) was linear for halibut >10 mm SL (Fig. 4).

Mortality estimates

I did not use data from the 1987 survey for estimating mortality because nearly all of the 1987 year-class occurred in bays and comparisons of mortality between bay and coast habitats were an essential step in the analysis. The relationship between abundance and age (estimated from the length-at-age relationship) of the 1988 year-class was used to estimate age-specific mortality rates.

I used seven different models to estimate age-specific instantaneous mortality rates. Three of the models were estimates based on the following assumptions regarding the relationship between survival rates and age (Barlow 1982): (1) Age-specific survival rates increase linearly with age; (2) age-specific survival rates increase exponentially with age; and (3) age-specific survival rates approach an asymptote with age. The two daily production models estimated age-specific instantaneous mortality rates based on the relationship between daily production (abundance of length class/duration of length class) and age (Lo 1985). The last

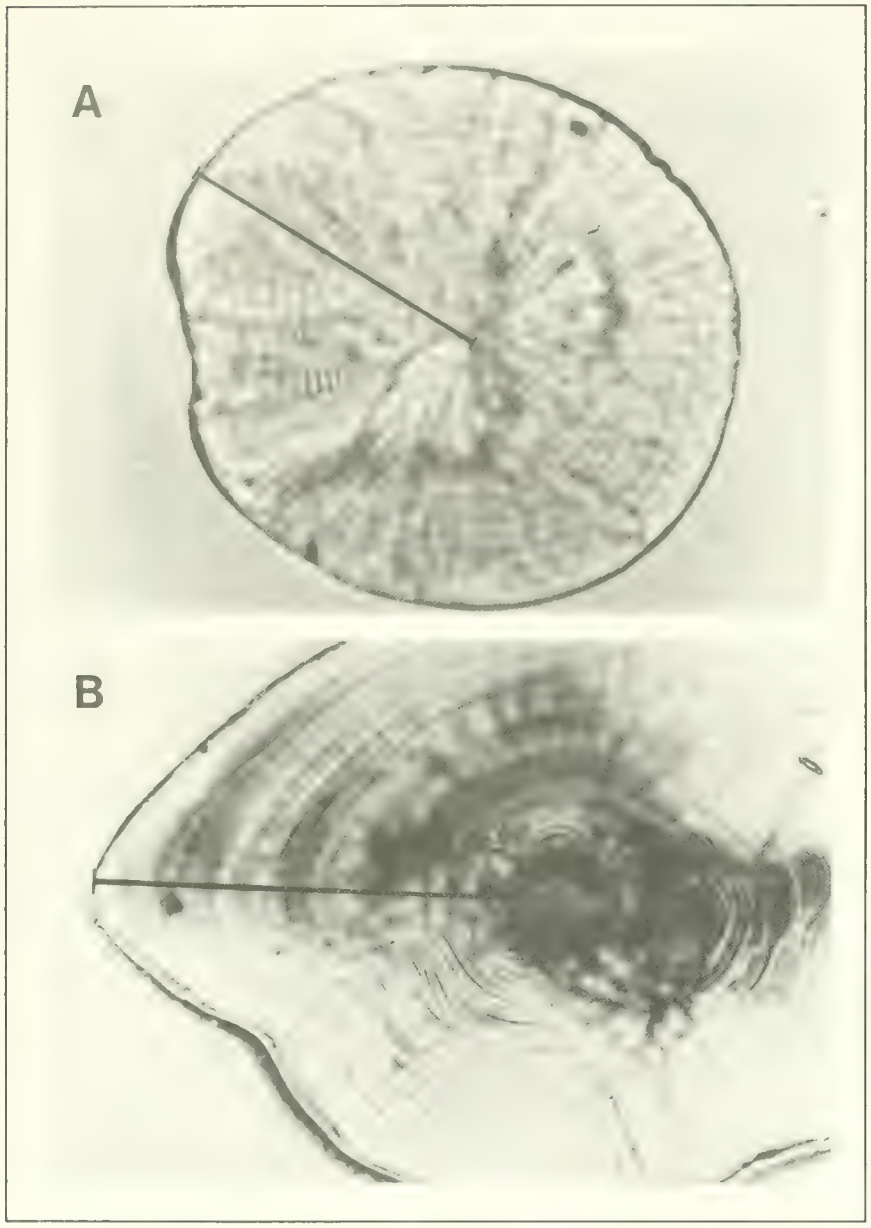

Figure 3
Photomicrographs of California halibut otoliths. (A) Sagitta from halibut 6.94 mm SL, estimated age 22 days. Distance of drawn radius, 70 μm. (B) Sagitta from halibut 48 mm SL, estimated age 109 days. Distance of drawn radius, 890 μm.

two models were simple linear estimates, using a linear regression of ln-transformed abundance-at-age on age (constant mortality rate with age) and on ln(age) (age-specific mortality rates). The sum of squared deviations of observed abundance-at-age from the calculated or transformed abundance-at-age predicted by each model was used to determine the model that best fit the data.

Mortality estimates for halibut from the open coast include loss of juveniles from the open coast population due to emigration into the bays. These estimates are used to calculate age-specific emigration rates by comparing the apparent mortality (= mortality + emigration) on the open coast to the total mortality calculated for the population on the open coast and in the bays.

Results

Effects of season and location on size-at-age

Relationships between halibut length and age did not vary significantly between seasons or between habitats. Analysis of covariance indicated no significant difference in length-at-age between fish that had birthdates in the spring and those with birthdates in the late summer and fall, but the sample size was small for fall fish (n 9) (Table 2). The common slope was 0.6206 (SE 0.0905).

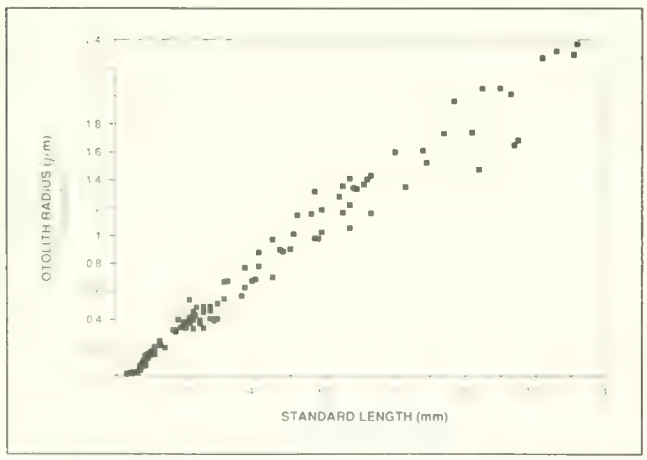

Figure 4
Relationship between otolith radius (μm) and standard length (mm) of California halibut (n 120).

Analysis of covariance also indicated no significant difference between juveniles from the bays and the open coast in the relationship between length and age (Table 2). The comparison was made between fish from the bays and the open coast. The common slope was 0.471 (SE 0.0238). Therefore, I used the pooled data for all estimates of growth (n 120).

Table 2

Regression analysis and analysis of covariance (ANCOVA) of size-at-age by season and by habitat. Slopes and intercepts were compared using ANCOVA; all tests were not significant at $P>0.05$.

Covariates	N	Size range (mm)	Equality of		F-statistic	
			Intercept	Slope	Intercept	Slope
Seasons						
Spring	26	27–80	−7.6	0.637	1.68	0.051
Fall	9	27–83	−8.6	0.594		
Habitats						
Coast	51	6.8–41	−7.2	0.468	3.87	0.035
Bays	26	8.3–41	−4.7	0.478		

Length-at-age

The relationship between standard length (mm) and age (days) was best described with the Gompertz growth function,

$$\text{Length} = P_1 \times \exp(P_2(1 - \exp(-P_3 \times \text{age})))$$

with $P_1 = 2.13$, $P_2 = 4.77$, and $P_3 = 0.011$, and an estimated mean square error of 0.99 ($2SE_{P_1} = 0.34$, $2SE_{P_2} = 0.137$, $2SE_{P_3} = 0.0013$) (Fig. 5A). The parameter P_1 closely estimates the length-at-hatching, which is 2.0 for halibut (Ahlstrom et al. 1984).

The relationship of age-at-length was determined with the function,

$$\text{Age} = -88.347 \times \ln(\ln(\text{standard length} \times 251.07)/-4.769)$$

derived from the Gompertz relationship for size-at-age (Methot 1981) (Fig. 5B). The variance in the estimate of age-at-length increases with increasing length; the 95% confidence interval (CI) for a halibut age 25 days is ± 6 days, but for a 90-day-old halibut the 95% CI is ± 19 days (Fig. 5). This relationship was used to convert length-classes into age-classes using the mean of each length-class (Lo 1985).

I used the method outlined by Methot (1981, equations 1–5) to compute the age-specific daily growth rates. Length-specific daily rate of growth and the variability in growth rate increased with increasing length: the slowest growth occurred just after transformation (SL 6–10 mm), with daily growth < 0.3 mm/day, and maximum growth rates of about 1 mm/day occurred in juveniles 70–120 mm SL (between 110 and 160 days) (Fig. 6). These growth rates are similar to those measured by Allen (1988) who estimated that juveniles 21–29 mm SL grew at 0.36 mm/day, and juveniles 19–47 mm SL grew at 0.99 mm/day.

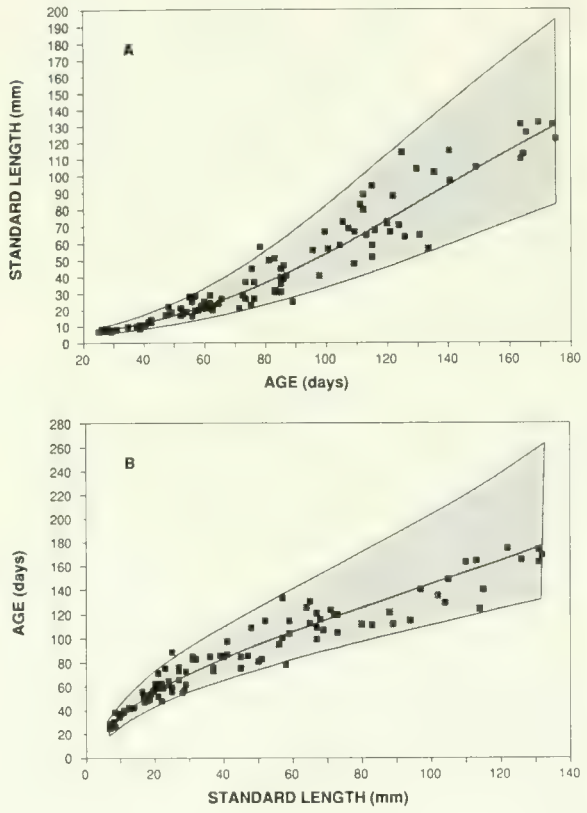

Figure 5

Gompertz relationship with 95% confidence intervals fitted to length-at-age of California halibut. (A) Standard length-at-age; (B) estimated age-at-length (mm).

Distribution and abundance

Juvenile California halibut 16–70 mm SL were present in the bays during January–July 1987 and March–September 1988, and on the open coast between May and September 1988. The distribution of transforming larvae and juveniles on the open coast differed for the 1987 and 1988 year-classes, with very few larvae and no small juveniles taken on the open coast in 1987,

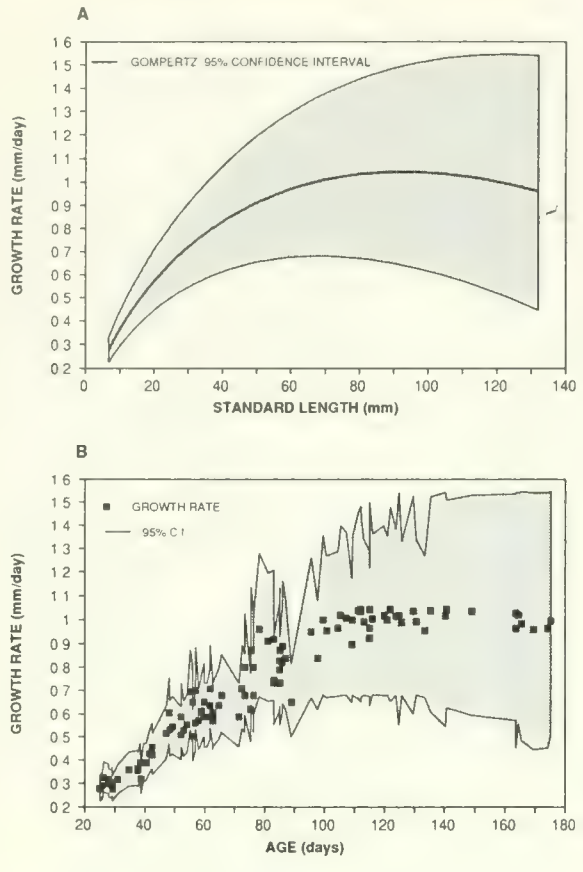

Figure 6

Growth rates of juvenile California halibut estimated from the Gompertz parameters for length-at-age, shown with 95% confidence intervals. (A) Relationship between growth rate (mm/day) and length (mm); (B) relationship between growth rate (mm/day) and age (days).

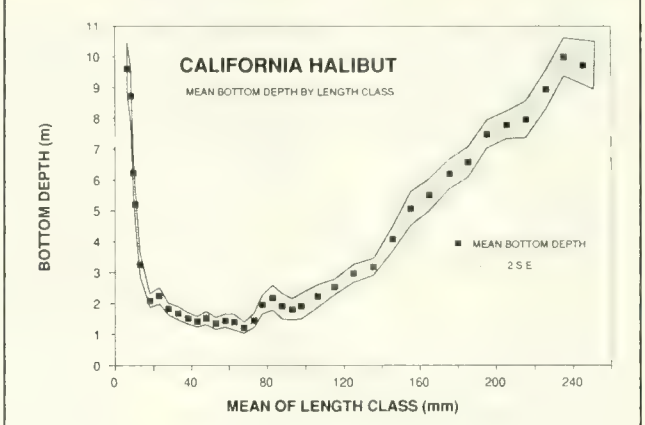

Figure 7

Mean depth of capture of California halibut by standard length-class (mm). Length-classes (mm) were ⩽7 (n 54), 8 (52), 9 (47), 10 (38), 11–15 (116), 16–20 (198), 21–25 (161), 26–30 (161), 31–35 (116), 36–40 (116), 41–45 (138), 46–50 (127), 51–55 (124), 56–60 (92), 61–65 (81), 66–70 (92), 71–75 (74), 76–80 (45), 81–85 (53), 86–90 (50), 91–95 (42), 96–100 (53), 101–110 (74), 111–120 (103), 121–130 (101), 131–140 (154), 141–150 (154), 151–160 (109), 161–170 (129), 171–180 (143), 181–190 (121), 191–200 (135), 201–210 (128), 211–220 (88), 221–230 (73), 231–240 (60), and 241–250 (47).

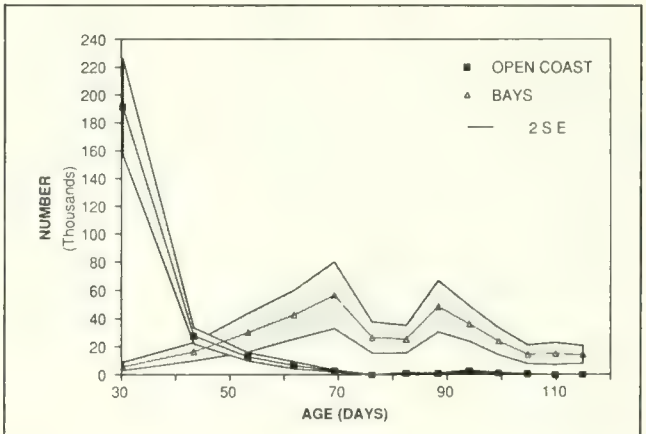

Figure 8

Abundance of juvenile California halibut by age-class for open coast and bay habitats in 1988.

whereas transforming larvae and newly-settled juveniles were common in 1988. Only the 1988 year-class was used to compare growth and mortality rates for juvenile halibut in bays and on the open coast. Further information on the distribution patterns of juvenile California halibut can be found in Kramer (1990).

The length distribution of transforming larval and juvenile halibut varied with depth. The smallest length-class of halibut (⩽7 mm SL) was taken at an average depth of 9.6 m (SD 3.08, N 54). The mean depth of occurrence decreased with increasing length up to a mean length of 67.8 mm SL (Fig. 7). At this size, the trend reversed, with mean depth of occurrence increasing with increasing length (Fig. 7). This pattern of length-at-depth indicates that transforming and newly-settled halibut move into shallower water along the open coast and into the bays, and halibut >70 mm SL move into deeper water habitats within the bays (maximum bay depths were <5 m) and eventually move out of the bays to the open coast (Fig. 7) (Plummer et al. 1983).

The age of peak abundance of juvenile halibut in the bays in 1988 was equivalent to the average time required for newly-hatched larvae to move from the continental shelf to the bays. Peak abundance was at about 70 days in both Mission Bay and Agua Hedionda

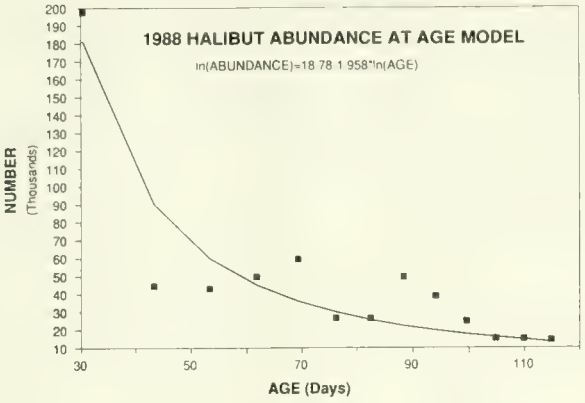

Figure 9

Total abundance of juvenile California halibut by age-class summed over both open coast and bay habitats, with the fitted model used to estimate mortality rates.

Table 3

Sum of squared deviations (SS) between observed and calculated or transformed abundance-at-age predicted from seven regression models applied to abundance-at-age for juvenile California halibut from 1988.

	Model	Residual SS ($\times 10^9$)
1	Survival rate (SR) increases linearly SR = 0.264 + 0.0072 * age	6.48
2	Survival rate increases exponentially SR = 0.174 * exp((0.0070 * age) + 1.0035)	7.99
3	Survival rate asymptotic SR = 0.025 * age * exp(−0.897)	7.49
4	Daily production ln(daily production) = 17.1 − 1.54 * ln(age)	12.09
5	Daily production ln(daily production) = 9.55 − 0.0123 * age	12.60
6	Log-transformed abundance on age ln(abundance) = 12.3 − 0.0229 * age	10.87
7	Log-transformed abundance on ln(age) ln(abundance) = 18.78 − 1.958 * ln(age)	4.38

Lagoon ($N_{\text{Mission Bay}}$ 42,067, SE 8543; $N_{\text{Agua Hedionda Lagoon}}$ 14,432, SE 3312), but there was a second large peak in Mission Bay for individuals at about 90 days (N 43,697, SE 7850) (Fig. 8).

The class composed of transforming larvae (age 30 days) was the most abundant age class on the open coast in 1988 (N 191,553, SE 17,339) (Fig. 8). Abundance rapidly decreased with age on the open coast, with essentially no halibut 70–180 days of age present on the open coast (Fig. 8). The decline in abundance of halibut on the open coast corresponded to an increase in the bays (Fig. 8).

Mortality

Total age-specific abundance was determined by combining data from the bay and open coast habitats (Fig. 9). In the survey area, the total loss of juvenile halibut ages 30–115 days was estimated at 183,250 (95% CL of 148,800 and 210,350) (Fig. 9).

Instantaneous mortality rates ($z_{(t)}$) were calculated by age-class using abundance-at-age, with age obtained from the linear regression of ln-transformed abundance on ln(age) (Table 3, Fig. 9), and the duration of each age-class calculated from the age-at-size relationship (Table 4) (Lo 1985). Instantaneous mortality rates ($z_{(t)}$) were highest (0.044) for the youngest juveniles, and decreased with increasing age but became constant ($\bar{x}$ 0.0124, SD 0.001) for juveniles 70 days of age and older (Table 4).

I also calculated habitat-specific instantaneous mortality rates ($z_{(t)}$) for juveniles ⩽70 days of age that were taken only on the open coast, and for those 88–115 days of age taken only in the bays (i.e., immigration completed (Table 5).

The apparent mortality in bays was much higher than that predicted from the combined bay and coast data, ranging from 0.043 to 0.037 for the bay model and from 0.011 to 0.014 for the total mortality model (Tables 4, 5). The age-specific mortality of halibut from the bays declined with increasing age, and was not constant as predicted by the total mortality model (Tables 4, 5).

To test for differences between the age-specific instantaneous mortality rates ($z_{(t)}$) of the total population, and of the open coast and bays, I used ANCOVA on the age-specific mortality coefficient, Beta. Beta is related to the instantaneous mortality rate ($z_{(t)}$) by the equation: $z_{(t)}$ = Beta/t (Lo 1985). The Beta coefficients for the total population (1.94, SE 0.22) and the open coast juveniles (ages ⩽70 days, Beta 3.58, SE 1.10) were significantly different ($P \leqslant 0.01$) (Table 6). The difference in the Beta coefficient between juvenile halibut on the open coast and the total halibut abundance-at-age is probably due to movement of halibut from the coast to the bays. Nearly half of the decline in abundance of juveniles along the coast could be caused by their movement into the bays (1.94/3.58 = 0.54). The Beta coefficients for the total population and the bay juveniles (ages 94–115 days) also differed significantly ($P \leqslant 0.05$), with a Beta of 0.69 (SE 0.77) for the total population, and 2.96 (SE 0.65) for the juveniles from the bays (Table 6). Mortality rates in the bays appear to be underestimated by the abundance-at-age model for the total halibut population.

Table 4

Instantaneous mortality rates for the 1988 year-class of juvenile halibut < 115 days ($z(t_i)$) by age in days (t_i) computed from daily juvenile production estimates (P_{ti}) and age (t_i) for 1988. Daily production estimates were obtained from log-linear model estimates of abundance-in-age classes adjusted for the number of days juveniles remained in the age-class. Percent of the total population in the bays by age-class is also given.

Length-class (SL, mm)	Age-class (t_i) (days)	Estimated abundance (n)	Percent in bays	Estimated daily production				
				P_{ti}	$P_{ti-1} - P_{ti}$	$t_i - t_{i-1}$	$t_i = (t_i + t_{i-1})/2$	$z(t_i)$
≤10	30.3	181385.1	3.08	18138.5				
11–15	43.3	90161.8	40.37	7706.1	10432.4	13.0	36.8	0.044
16–20	53.3	60025.3	69.92	6454.3	1251.8	10.0	48.3	0.016
21–25	61.8	44927.3	86.16	5615.9	838.4	8.5	57.5	0.015
26–30	69.3	35901.3	95.24	5056.5	559.4	7.5	65.5	0.013
31–35	76.2	29812.5	100.00	4586.5	469.9	6.9	72.7	0.013
36–40	82.5	25518.1	95.93	4183.3	403.2	6.3	79.3	0.013
41–45	88.4	22290.1	98.13	3910.5	272.7	5.9	85.4	0.011
46–50	94.1	19723.2	93.30	3586.0	324.5	5.7	91.2	0.014
51–55	99.5	17681.8	95.68	3336.2	249.8	5.4	96.8	0.012
56–60	104.8	15973.4	96.17	3132.0	204.2	5.3	102.1	0.011
61–65	109.9	14554.3	100.00	2910.8	221.2	5.1	107.3	0.013
66–70	114.9	13340.1	100.00	2722.4	188.4	5.0	112.4	0.012

Table 5

Habitat-specific instantaneous mortality rates of juvenile halibut < 115 days ($z(t_i)$) by age in days (t_i) computed from daily juvenile production estimates (P_{ti}) and age (t_i) for 1988. Halibut 30.3–69.3 days of age were from the open coast habitat, and halibut ≥88.4 days were from the bays. Daily production estimates were obtained from log-linear model estimates of abundance by habitat adjusted for the number of days juveniles remained in each age-class.

Habitat	Age-class (t_i) (days)	Estimated abundance (n)	Estimated daily production				
			P_{ti}	$P_{ti-1} - P_{ti}$	$t_i - t_{i-1}$	$t_i = (t_i + t_{i-1})/2$	$z(t_i)$
Open coast	30.3	185384.8	18538.5				
	43.3	32540.9	2781.3	15757.2	13.0	36.8	0.065
	53.3	11820.4	1271.0	1510.3	10.0	48.3	0.054
	61.8	5746.9	718.4	552.6	8.5	57.5	0.051
	69.3	3288.5	463.2	255.2	7.5	65.5	0.048
	76.2						
	82.5						
Bays	88.4	45824.8	8039.4				
	94.1	33279.7	6050.9	1988.6	5.7	91.2	0.043
	99.5	25010.6	4718.9	1331.9	5.4	96.8	0.041
	104.8	19175.6	3759.9	959.1	5.3	102.1	0.038
	109.9	15035.1	3007.0	752.9	5.1	107.3	0.039
	114.9	11972.7	2443.4	563.6	5.0	112.4	0.037

Bay abundance-at-age estimate: $\ln(\text{abundance}) = 33.68 - 5.12 * \ln(\text{age})$ (residual SS = 4.567×10^7).
Open coast abundance-at-age estimate: $\ln(\text{abundance}) = 28.76 - 4.87 * \ln(\text{age})$ (residual SS = 6.219×10^7).

Table 6

Analysis of covariance (ANCOVA) on the age-specific mortality rate Beta by habitat, where Beta is defined by the relationship between the instantaneous mortality rate and age (z_t = Beta/t).

Covariates	N	Age range (days)	Beta	SE	F	P
Total population	4	43–69	1.94	0.22	19.62	<0.01
Coast population	4	43–69	3.58	1.10		
Total population	5	94–115	0.69	0.76	8.31	<0.05
Bay population	5	94–115	2.96	0.65		

Rate of movements into bays

I estimated the proportion of the population by age-class emigrating each day from the open coast to the bays by calculating the difference between the percentage of juvenile halibut lost daily from the total population and from the open coast using age-specific instantaneous mortality rates (Tables 4, 5) in the following equation:

$$\% \text{ emigrating/day} = ((1 - e^{-z(\text{total population})} - (1 - e^{-z(\text{open coast})})) \times 100.$$

The decline in abundance of juvenile halibut on the open coast between days 30 and 70 was 182,100, and for the total population was 145,500 (Tables 4, 5). During this time, the daily emigration rate increased from 1.99% for juveniles from age 30–43 days, to 3.67% from age 43–53 days, then declined slightly to 3.35% by 70 days.

Discussion

Extent of bay utilization

Juvenile halibut appear to be dependent upon bays as nursery areas, since nearly all halibut between 76 and 115 days of age occurred in the bays rather than the open coast (Fig. 8). Transforming larvae and newly-settled juvenile halibut ≤70 days old occurred on the open coast (97% of the transforming larvae were on the open coast), but over 95% of the total population of halibut >70 days were in the bays (Table 4).

An alternative explanation for the decline in abundance of juvenile halibut on the open coast is that they move somewhere other than the bays, or suffer heavy mortality. If halibut moved offshore, one would expect a positive relationship between size of juvenile halibut (31–70 mm SL, or 76–115 days) and bottom depth. This is contrary to the observed size-structured distribution pattern (Fig. 7). The decrease in abundance of juvenile halibut on the open coast may have included higher in situ mortality rates, but the corresponding increase in abundance in the bays suggests that movement from the coast to the bays probably accounts for about half of the coastal decline.

Advantage of bays as nursery areas

Growth The potential advantages of using bays as nursery areas are increased growth and decreased mortality. Increased growth was not observed for juvenile English sole *Parophrys vetulus* in Oregon estuaries: they grow at about the same rate as juveniles on the Oregon coast, but were more variable in size-at-age than those on the coast (Rosenberg 1982). Similarly, growth rates of juvenile California halibut ≤40 mm SL on the coast and in the bays were not significantly different.

California halibut 70–120 mm SL grew faster than all other length-classes with rates approaching 1 mm/day (Fig. 6). These fast and variable growth rates occurred during the period when juvenile halibut occurred only in the bays (>115 days of age). Unfortunately, comparisons could not be made between open coast and bay habitats during this period of fast growth, which coincides approximately with a change in the food habits of halibut >55 mm SL, from a diet composed primarily of small crustaceans (copepods, amphipods, mysids, and cumaceans) to one composed of an increasing proportion of fish by weight (mostly gobies) (Haaker 1975, Allen 1988, Drawbridge 1990). Juvenile halibut feeding on gobies in the laboratory remain partially buried in the substrate, only striking at gobies passing within a distance of three headlengths (Haaker 1975). Gobies are abundant in bays (mean density of *Ilypnus gilberti* in Mission Bay, 8.1/m^2), but not in shallow coastal waters <30 m (Brothers 1975, Allen 1985, Plummer et al. 1983). The diet of larger juvenile halibut becomes increasingly piscivorous: juvenile halibut >150 mm SL on the open coast eat primarily northern anchovies by weight (Plummer et al. 1983, Allen 1982).

Predation risk Predation risk may be higher for small halibut on the open coast than in the bays. At least six fish species on the open coast are known to eat flatfishes: these include California halibut, thornback ray *Platyrhinoidis triseriata*, fantail sole *Xystreurys liolepis*, bigmouth sole *Hippoglossina stomata*, speckled sanddab *Citharichthys stigmaeus*, and California lizardfish *Synodus lucioceps* (Ford 1965, Allen 1982). Ford (1965) found many small halibut (TL <10 mm) in the stomach contents of thornback rays, with a maximum of 15 newly-settled halibut in the stomach of one ray alone. The combined density of rays *Platyrhinoidis triseriata*, *Urolophus halleri*, and *Gymnura marmorata*) on the shallow open coast (<10 m) is about 100/hectare (Ford 1965). Speckled sanddab is the most abundant flatfish in shallow open coast waters, with a mean density of 950/hectare at Torrey Pines (Ford 1965, Allen 1982, Love et al. 1986, DeMartini and Allen 1984, Kramer 1990). Although the diet of speckled sanddab is composed primarily of mysids, they are probably capable of eating newly-settled halibut, since small unidentified flatfish juveniles have been found in their stomachs (Ford 1965).

In the bays, two potential predators include the round stingray *Urolophus halleri*, and the staghorn sculpin *Leptocottus armatus* (Allen 1985, Tasto 1975, Babel

1967). Both occur along the shallow open coast as well, but are most abundant in bays (Allen 1985). Staghorn sculpin feed primarily on crustaceans (>50% by weight), but small diamond turbot *Hypsopsetta guttulata* have also been found in their stomachs (frequency of occurrence 0.5%) (Tasto 1975). Over 94% of the diet by volume of round stingray is composed of molluscs, polychaetes, and crustaceans, but gobies also have been found in their stomachs (Babel 1967).

Other predators found both in the bays and on the open coast include barred sand bass *Paralabrax nebulifer*, spotted sand bass *P. maculatofasciatus*, and kelp bass *P. clathratus*. Spotted sand bass occur predominantly in bay habitats, barred sand bass occur ubiquitously in the bays and on the open coast, and kelp bass are associated with rock reef and kelp bed habitats on the open coast, but also have been taken as juveniles in bays (Allen 1985, Lane 1975). Kelp bass on the open coast feed mostly on northern anchovies and crabs, and have been found occasionally with flatfishes in their stomachs (Quast 1968). The diet of barred sand bass taken from bottom depths of 8–30 m on the open coast indicates that they forage close to the substrate, feeding on brachyuran crabs, mysids, pelecypods, and epibenthic fishes (mostly *Porichthys notatus*) (Roberts et al. 1984, Feder et al. 1974). Spotted sand bass occur predominantly in bay habitats, feeding on crabs and other crustaceans, and on small kelpfish (Feder et al. 1974, Allen 1985). The juveniles of all three species are found commonly in Mission Bay, and are considered highly probable goby predators (Brothers 1975). The sand basses probably eat juvenile halibut also, as gobies and halibut share the same habitats.

Comparison of predation risk must also include a measure of abundance or biomass of predators by habitat. The estimated density of the potential bay predators (round stingray, *Paralabrax* spp., and staghorn sculpin) based on otter trawl surveys is 61/hectare in Agua Hedionda Lagoon, and only 3/hectare on the open coast (San Diego Gas and Electric 1980). The estimated density of two open-coast predators, the speckled sanddab and the thornback ray, is >1000/hectare (Ford 1965). Based on this scanty information, it appears that predators are more abundant on the open coast than in the bays.

Thus the possible advantages of using bays as nursery areas by juvenile halibut appear to be at least twofold: (1) Decreased risk of predation on newly-settled juveniles, since fewer predators are known to occur there; and (2) increased potential for faster growth of juveniles >55 mm SL because small fishes (gobies) are more abundant in bays than on the open coast (Haaker 1975, Allen 1985).

Migration to bays

The migration of larvae from spawning areas over the continental shelf to their juvenile nursery areas in embayments is thought to consist of two phases (Boehlert and Mundy 1988): Accumulation of larvae in the nearshore zone (Boehlert and Mundy 1988, Miller et al. 1986), and location and entering of the bays by transforming larvae and juveniles (Boehlert and Mundy 1988). The nearshore accumulation of larvae prior to movement to the bays is probably facilitated by the timing of spawning, the short duration of pelagic stages, and the vertical distributions of the postflexion and transforming larval stages. California halibut spawn throughout the year, with peak spawning during the winter and spring (Lavenberg et al. 1986, Walker et al. 1987). The spawning peak coincides with the period of minimum offshore transport of surface water in the Southern California Bight (Parrish et al. 1981, Jackson 1986). Offshore transport increases in late spring and summer due to increasing upwelling activity (Parrish et al. 1981, Jackson 1986). The seasonal shift in upwelling activity has been correlated with a seasonal cross-shelf shift in the zooplankton assemblage off San Onofre: from February to early April the community was shifted onshore, and from mid-April to July the shift was offshore, corresponding to the period of increased upwelling (Barnett and Jahn 1987).

The size distribution of California halibut larvae taken in plankton tows indicates that they move inshore as they approach metamorphosis. Preflexion and flexion larvae (~2–6 mm SL) occur in midwater >2 km offshore, whereas transforming larvae occur at night in the neuston within 1 km of shore (Moser and Watson 1990). My collections indicated that transforming larvae occur on the bottom during the day; thus transforming larvae appear to undergo a daily vertical migration, occurring at the surface at night and at the bottom during the day. Larvae of other *Paralichthys* species, yellowtail flounder *Limanda ferruginea*, stone flounder *Kareius bicoloratus*, and the larval stages of several crustacean taxa have similar diurnal activity patterns (Weinstein et al 1980, Tsuruta 1978, Shanks 1988, Penn 1975, Smith et al. 1978).

Postflexion and transforming halibut larvae may be transported shoreward by internal waves at night when they are in the neuston, with very little movement during the day while they are on the bottom, resulting in accumulation of larvae nearshore (Moser and Watson 1990). Surface slicks associated with internal waves may transport neustonic larval fishes and crustaceans onshore (Shanks 1988, Kingsford and Choat 1986). Recovery of drift bottles released <20 miles offshore in the Southern California Bight region is greatest

between March and October, also suggesting increased onshore transport of surface water (Schwartzlose 1963).

Once nearshore, transforming larvae or settled juveniles may search for bays by using longshore transport (Boehlert and Mundy 1988). Net longshore transport of shallow shelf waters in the Southern California Bight is to the south (Winant and Bratkovich 1981). Longshore current speed measured in shallow water (15m) averages less than 5cm/second; at this speed, after 12 hours longshore movement could be as great as 2km (Winant and Bratovich 1981).

My data on the abundance of transforming larvae and newly-settled juveniles provide an estimate of the time required for halibut to locate and enter the bays from the open coast. The time required can be considered to be equivalent to the difference in the age of peak abundance between the coast and the bays. Halibut reached peak abundance in the bays at an age of about 70 days in 1988, whereas they were most abundant at age 30 days (transformation) on the open coast (Fig. 8). Thus the time required to locate and enter the bays was about 40 days in 1988 (70–30 = 40 days) (Fig. 8). Over a 40-day period, halibut potentially could be transported about 80km alongshore (40 days × (2km at 12 hours in the neuston)), which is greater than the total distance between the northern sampling block at San Onofre and Mission Bay (64km) (Fig. 1). I measured the maximum distance between adjacent bays in southern California at less than 60km, thus larvae using this transport mechanism would probably encounter a bay within 30 days of reaching the shallow-water coastal environment.

The potential cues used to find the entrances to bays include temperature, currents, odor, turbidity, and bottom substrate (Boehlert and Mundy 1988). A probable cue in southern California is temperature: during spring and summer, when larvae and juveniles are moving into the bays, the temperature is as much as 5°C warmer in the bays than on the open coast (Kramer 1990).

Once a bay entrance is located, the mechanism used to migrate into the bay probably is tidal transport, using incoming tidal currents to aid movement into the bay, and remaining at the bottom to avoid transport out of the bay (Weinstein et al. 1980, Boehlert and Mundy 1988, Fujii et. al. 1989, Tsuruta 1978, Weihs 1978, Runsdorp et al. 1985). To use tidal stream transport to move into bays, individuals must be able to orient to currents, control vertical movements, and remain on the bottom during unfavorable currents. These abilities probably develop by the time larvae reach transformation (Boehlert and Mundy 1988, Weinstein et al. 1980). Only a few tidal cycles may be required for halibut to move from the entrance into the bay. Larval flounder (*Paralichthys* sp.) on the North Carolina coast use tides to augment movement into marshes, migrating to the surface during night flood tides and remaining on the bottom during ebb tides and during the day (Weinstein et al. 1980).

In conclusion, California halibut settle either in bays or on the open coast, but ultimately nearly all halibut settling on the coast enter and use the bays as nursery areas during their first year of life. The advantages of bays as nursery areas may be a decrease in risk of mortality of newly-settled halibut, and an increase in growth of larger juveniles that feed upon the abundant small fishes in the bays.

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Abstract.– The larvae and juveniles of two platytroctid species, *Holtbyrnia latifrons* and *Sagamichthys abei*, from the northeastern Pacific are described. Young individuals were collected at a broad range of mesopelagic depths, indicating that they occupy similar depths as adults. The relatively large larvae (~15 mm) have well-developed teeth and fins while carrying the yolksac. Presence of <20 mm sizes from most months of the year may indicate year-round spawning.

Description of Young of the Mesopelagic Platytroctids *Holtbyrnia latifrons* and *Sagamichthys abei* (Pisces, Alepocephaloidea) from the Northeastern Pacific Ocean

Tetsuo Matsui

Marine Life Research Group
Scripps Institution of Oceanography A-027
La Jolla, California 92093

The only published description of larval platytroctids is that of Beebe (1933). However, Parr (1960) in his review of the family (then known as Searsidae) believed larval platytroctids of 11–17 mm could not be identified even to genus, and showed that Beebe's detailed description of the larvae identified as *Bathytroctes rostratus* was based on several species. In a recent revision of the family, Matsui and Rosenblatt (1987) recognized five species off California. None are congeners. The earliest larvae of the two commonest species, *Holtbyrnia latifrons** and *Sagamichthys abei*, are identifiable by their photophores. This report describes the young of *H. latifrons* and *S. abei* and presents catch data from the Scripps Institution of Oceanography (SIO) Fish Collection and depth of capture data from a series of opening-closing net tows.

Material and methods

Material used in this study is from the SIO Fish Collection and from samples collected on seven cruises sponsored by the Marine Life Research Group (MLRG) of SIO. Most SIO Fish Collection samples and some from the MLRG cruises were captured in 3-m Isaacs-Kidd midwater trawls (IKMT). Other MLRG collections were made with 2-m Stramin nets and 1-m plankton nets. The 1-m nets were attached to modified Leavitt devices (Leavitt 1938) that allowed the nets to be opened and closed by messengers to sample discrete depth intervals. Their sampling depths were either recorded by TSK depth-distance recorders on the nets and activated when the nets were sampling, or estimated from records taken on a Benthos time-depth recorder attached to the bottom net in the cast. Eight depth intervals from surface to nearbottom were sampled at stations 850–1350 m deep, and 12 depth intervals at stations of 1370 m to ~1800 m. Two samples in the Fish Collection were taken in opening-closing Bongo nets (McGowan and Brown 1966).

A total of 167 (young and adult) *H. latifrons* and 220 *S. abei* were examined in the study. The description of *H. latifrons* is based on measurements and counts of 157 individuals (1 larva, 12 transitional specimens, and 144 juveniles). For *S. abei*, 1 larva, 4 transitional specimens, and 37 juveniles were measured and counted. Samples of *H. latifrons* were gener-

* *Holtbyrnia latifrons* may be a junior synonym of *H. baucoti* Mayer and Nalbant 1972. However *H. baucoti* was inadequately described, and I have failed to gain additional information on the holotype.

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ally collected near the coast at 22–38°N, off the west coast of California and Baja California (but mainly 28–33°N). Samples of *S. abei* were also collected near the coast at 28–38°N, with one individual from 4°N, 142°W.

Most specimens were initially preserved in formaldehyde and later transferred to 70% isopropanol. Length measurements of small specimens were taken with an ocular micrometer of a dissecting microscope and by dividers for larger measurements. All *S. abei* and *H. latifrons* examined had a flexed notochord. Since the notochord extended more than 1 mm beyond the hypurals in the earlier stages, the standard length (SL) measurements of the larvae were taken from the snout to posterior tip of notochord, or to the most posterior extension of the hypurals, whichever was greater.

Head length (HL) measurements were taken from the tip of the snout to the posterior margin of opercle. In individuals with torn or curled gill covers, the anterior base of pectoral fin was substituted as the posterior reference point for HL.

Photophore nomenclature follows Parr (1960) as modified in Matsui and Rosenblatt (1971).

Key to young platytroctids off California

1a Photophores (or melanophores in the shape of photophores) in gular region (GO_2; Figs. 1, 2) from yolksac through later juvenile stages **2**

1b Neither photophores nor patch of melanophores in gular region **3**

2a Photophores and silvery reflector present on anterior dorsal margin of eye (OO) and on subopercle (SBO) from yolksac stage; intraventral photophore (IVO) present from yolksac stage; opercular opening extending dorsally to about mideye; body coloration generally whitish blue ..... ***Sagamichthys abei***

2b OO and SBO photophores absent; IVO appearing near end of yolksac stage; opercular opening extending dorsally to top of eye; epidermal layer lightly pigmented from yolksac stage, becoming dark-brown in juvenile ..... ***Holtbynia latifrons***

3a Broad edentulous space between innermost tooth of each premaxilla; small photophore between bases of pelvic fins (IVO) present after yolk is resorbed; gill opening extending dorsally to a level with top of eye ..... ***Maulisia argipalla***

3b Only narrow edentulous space between innermost tooth of each premaxilla; photophores absent; gill opening on a level with mideye **4**

4a Nasal sac nearly bordering maxilla; premaxilla not meeting medially with part extending laterally ..... ***Pellisolus eubranchus***

4b Nasal sac midlength of snout; premaxilla meeting medially, with none along lateral margin of mouth ..... ***Mirorictus taningi***

Description

Holtbyrnia latifrons (Fig. 1)

Pigmentation The least developed individual examined has pigmented eyes, pigmentation on the shoulder organ and at the site of the posterior gular organ (GO_2); the posterior margin of opercle and the dorsal portion of yolksac are lightly pigmented (Fig. 1A). This is the only specimen examined that is considered a larva; the remaining yolksac stages are already beginning to form the juvenile pigment pattern, and are termed transitional individuals. The most prominent pigmentation in these is the black tissue lining the digestive tract from the mouth and branchial chamber to the anus. Melanophores are concentrated at the dorsal and ventral margins, and on the fins and fin bases. Pigmentation increases with size, and in late juveniles the entire body as well as the head (except for the translucent top of skull) is nearly black in color.

Morphometrics The larva (Fig. 1A) has a small head and mouth and an oblong eye that is nearly twice as long horizontally as vertically. The transitional specimen (Fig. 1B) is much more adult-like with the head and eyes nearly doubling in size, and the eyes almost round.

Much of the growth in transition stages is in the head region, and although the body length of 12–17 mm

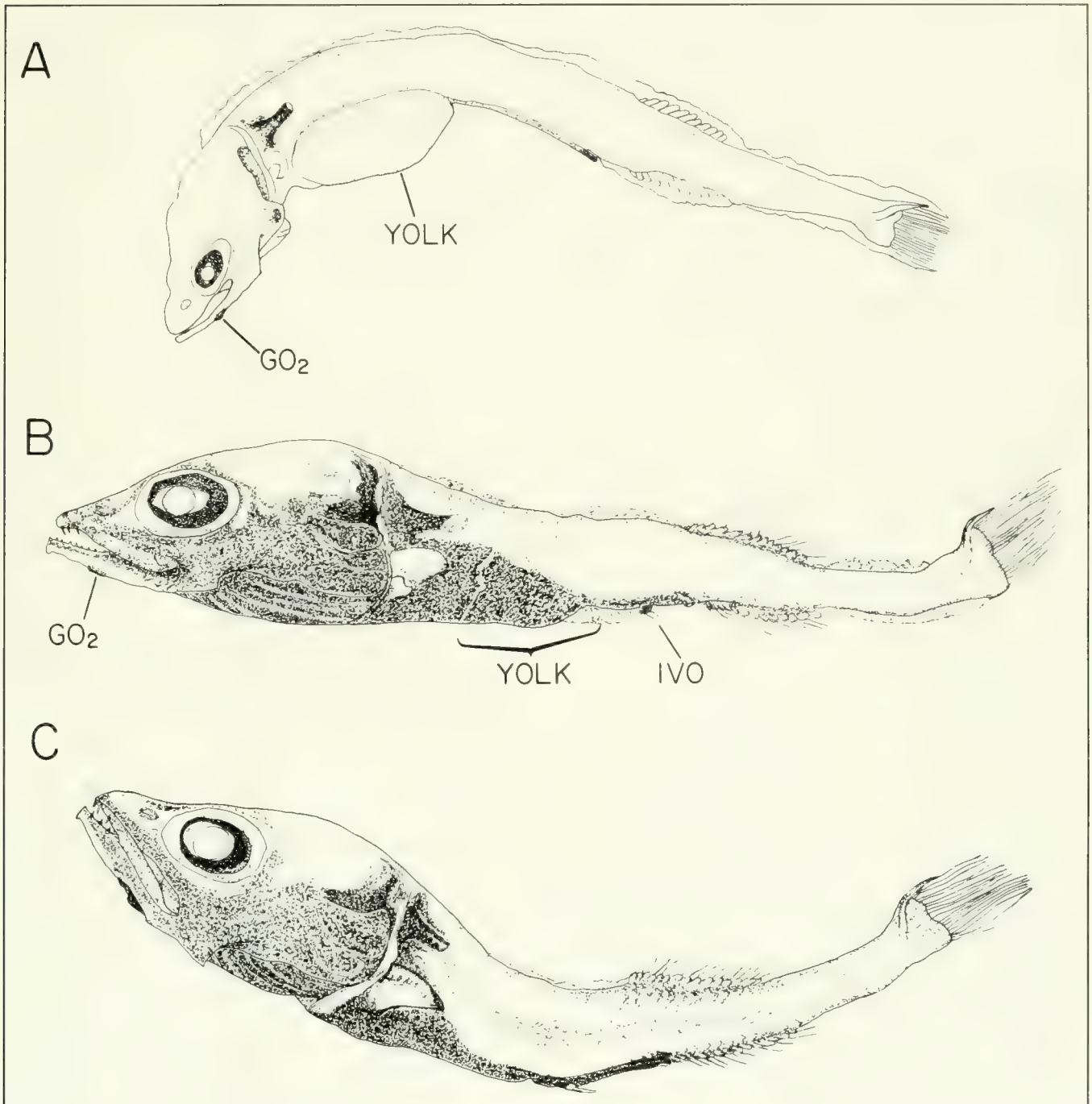

Figure 1

Camera lucida drawings of the young of *Holtbyrnia latifrons*: (A) M1-2-1, 15-mm larva; (B) SIO 65-439, 14-mm transitional specimen; (C) 65-443, 14-mm juvenile. GO_2 = posterior gular organ; IVO = intraventral organ.

juveniles is shorter than that of the larva, their head length is two times greater (Table 1). Head length increased from 15% of SL in the larva to the adult proportion of 30% of SL at the end of the transitional period. Head length of juveniles is proportionately larger than that of adults even from the earliest stages, measuring 29–37% of SL in the 12–18 mm SL range, with maximum of >40% SL at 36–45 mm SL (Table 2). Head depth increased from 9% SL in the larva, to 10–17% SL in transitional specimens, to 16–23% SL in juveniles as large as 50 mm.

Table 1

Measurements (in mm) and counts of *Holtbyrnia latifrons*. SL = standard length, HL = head length, Hd = head depth at angular, asterisks = SIO.

	Sample no.												
	M1-2-1	M11-1-3	M2-A7	M10-1R-2	M13st1	*67-62	*63-447	*65-439	*63-447	*66-398	*65-443	M7st3	*67-101
Lengths													
SL	15	15	15	14	14	13	14	14	14	14	14	16	16
HL	2.3	3.8	3.3	2.4	2.3	3.0	4.2	4.8	3.8	4.3	4.5	5.1	6.0
SL minus HL	13	11	12	12	12	10	10	8.9	11	9.3	9.2	10	9.7
Hd	1.4	1.4	1.7	1.4	1.2	1.4	2.0	2.3	1.8	2.2	2.4	2.7	2.9
Yolksac	3.7	3.6	3.3	3.2	3.0	3.0	2.6	2.5	2.3	0	0	0	0
Eye (long.)	0.72	0.92	0.91	1.1	0.76	1.0	1.3	1.6	1.3	1.5	1.4	1.6	2.0
Eye (vert.)	0.48	0.60	0.58	1.0	0.44	0.52	0.83	0.83	0.52	0.83	0.92	0.75	1.2
Maxilla	1.1	1.4	1.2	1.2	1.0	1.3	1.5	2.1	1.7	1.7	2.1	2.1	2.5
Counts													
Dorsal rays	0	11	15	14	14	12	16	13	16	15	16	18	19
Anal rays	0	10	13	10	–	13	13	13	14	15	14	16	12
Pectoral rays	0	0	0	0	0	0	0	0+2	0	–	4+?	4+?	4+?
Branchiostegals	2	4	5	8	8	8	8	8	8	8	8	8	8
Gill rakers	0	0	0+2	0	0	0+3	1+10	1+11	0+8	2+12	2+12	2+13	3+13
Pseudobranchiae	2	2	2	2	2	2	2	2	2	2	2	2	2
Dentition													
Vomerine	0	0	0	0	1	0	2	2	2	1	2	2	2
Palatine	0	0	0	0	0	0	1+1	1+1	1+1	1+1	1+2	1+1	1+1
Basihyal	0	0	0	0	0	0	1	1	0	0	0	0	1
Dentary	0	0	3+3	0	1+1	0	7+9	12+12	7+7	10+10	10+12	13+17	10+12
Mid-dentary	0	0	0	0	0	0	1+1	0	0	1+1	0+1	2+0	2+1
Maxillary	0	0	0	0	0	0	2+1	1+1	0	0	0	2+1	3+3
Premaxillary	0	0	0	0	0	1+1	2+2	3+4	4+3	3+5	4+5	5+5	4+3

Table 2

Summmarized counts and morphometrics (% SL) of *Holtbyrnia latifrons*. SL = standard length, HL = head length, Hd = head depth at angular.

			Dentition								% SL			
SL (mm)	Gill rakers	Pseudo-branchiae	Vomer-ine	Pala-tine	Pre-maxillary	Max-illary	Dentary	Mid-dentary	Basi-hyal	Basi-branchial	HL	Hd	Eye	Max-illary
Yolksac	0–1+0–11	2	0–2	0–1	0–4	0–2	0–12	0–1	0–1	0	15–35	8–17	5–11	7–15
12–15	1–3+11–14	2	1–2	1	4–5	0–5	7–12	0–2	0–1	0	29–33	15–19	9–12	12–15
16–20	2–5+13–15	2–4	2–3	1–2	4–6	2–8	10–24	0–6	0–4	0	29–42	14–19	7–13	11–16
21–25	2–5+13–17	2–4	2–5	1–2	4–8	5–16	15–27	0–2	0–4	0	33–39	16–20	10–12	14–17
26–30	5–7+16–19	4–5	1–2	1–2	4–9	5–19	16–30	0–5	0–3	0	35–45	17–23	11–13	14–20
31–35	6–7+16–17	5	2–4	1–2	7–10	5–23	15–26	0–5	0–2	0	36–39	16–19	11–12	17–20
36–40	6–8+18–19	6	1–2	1–4	6–9	11–33	19–23	4–5	0–2	0–1	38–42	19–20	10–12	18–21
41–45	7–9+18–21	5–6	2–3	1–4	7–11	11–33	20–27	3–6	0–1	0–5	38–42	19–22	10–13	17–20
46–50	7–8+18–19	8	2–3	1–4	10–12	15–32	33–40	2–4	0–1	0–4	36–42	19–21	10–11	18–21
51–55	7+19	7	2–3	2	9	27–29	30–34	1–4	0–1	0–5	37	20	11	21

Eye length increased from about 5% SL in the larva to as much as 11% SL in some of the transitional specimens and to 11–13% SL in 20–45 mm juveniles. Maxilla length increased from 7% of SL in the larva, to 9–15% SL during transition, to 17–21% SL in 30–50 mm juveniles.

Fins All specimens had the notochord flexed with 19 principal caudal rays present. In larvae, narrow finfolds extend anteriorly along the dorsal (to head) and ventral (to anus) body margins. Only the basal parts of the dorsal and anal rays are discernible on the larva (Fig. 1A), but there are 10–13 anal and 11–16 dorsal rays in

the transitional specimens (Table 1). Two pelvic rays are discernible in the most advanced transitional specimen (SIO65-439). Adult counts of dorsal (17–20), anal (14–16), and pelvic (9) fin rays are usually present in 30-mm juveniles. Pectoral fin rays form last, with the first rays appearing at approximately 23 mm SL and adult counts (16–20) by 45 mm SL.

Branchial region Branchiostegal rays appear early and only the larval specimen and the least developed transitional specimen had fewer than the adult count of 8.

Gill rakers are absent in the larva, but as many as 12 are on one side of the 1st gill arch in the transitional specimen. Nearly all of these gill rakers are on the lower arch. Only one transitional specimen (SIO65-439) had gill rakers on the 1st epibranchial. The lowest count for juveniles was 1 on the epibranchial and 12 total on the 1st arch, and ranged from 1 to 5 on the upper arch and 12 to 19 total in juveniles <20 mm SL. The smallest individual with the adult gill raker count of 25 was 27 mm SL and all individuals 42 mm and larger had counts in the adult range of 25–30.

Medial gill rakers of the 3d and 4th arches are in an uninterrupted row in juveniles as small as 19 mm, but no medial gill rakers form on the 1st and 2d arches until after 20 mm. By 45 mm SL, there are about 6 medial rakers on the epibranchial and on the ceratobranchial of the 2d arch, and 5 on these elements of the 1st arch.

There are 2 pseudobranchiae in the larva and transitional specimens. The smallest individual with a 3d pseudobranchium measured 17 mm and the smallest with a 4th was 20 mm. No specimen <50 mm SL had attained the highest adult count of 8. Counts varied as much as 4 between individuals of similar lengths.

Dentition In the study material, only the larva is toothless. Teeth on dentary, premaxilla, maxilla, vomer, palatines, basihyal, and on the lateral face of the dentary (mid-dentary teeth) appear during transition. Teeth are easily dislodged, contributing substantially to individual variation in counts. The most advanced transitional specimen (SIO65-439; Table 1) had a single medial tooth on the basihyal, a tooth on each palatine, and a total of 7 premaxillary, 2 maxillary, 24 dentary, and 2 vomerine teeth. Only one transitional specimen had mid-dentary teeth. There are fewer maxillary than dentary teeth in the early stages, but this gradually changes and the numbers are about even in individuals 25 mm and larger (Table 2). Highest count of premaxillary teeth among transitional individuals was 4 on a side. The numbers increased to 4–6 in 13–20 mm juveniles, with counts as high as 10 at 50 mm SL. The inner pair of premaxillary teeth point horizontally beginning from about 25 mm SL. Frequently, a second smaller tooth forms adjacent to the 1st.

Mid-dentary teeth are probably more susceptible to damage than other dentition and most individuals smaller than 30 mm were without them, although counts of 4 on one side occurred as early as 17 mm. Individuals 30–50 mm long usually had 4–5 mid-dentary teeth. In the youngest stages, a single tooth was usually present on each palatine. The number variably increased to as many as 4 in individuals over 30 mm. Most prejuveniles and early juveniles had a medial tooth on the basihyal, with occasional individuals with 2–4 in a medial row. Basibranchial and mesopterygoid teeth appeared after 40 mm, and ectopterygoid teeth were only found in the adults.

Photophores Photophores of young platytroctids are oriented horizontally (Matsui and Rosenblatt 1971). The posterior gular organ (GO_2; Fig. 1) is the only photophore present during most of the yolksac stage. It is an opaque spot outlined by dark pigment in the larva, and forms at the posterior, narrow end of a black, conically-shaped pouch. Near the end of the yolksac stage, the intraventral organ (IVO) develops inside a silver-lined, anteriorly facing pouch. The photophore at the subopercle (SBO) appears later in juveniles. However, it is considered rudimentary as it is surrounded by opaque tissue and is without an anterior opening. These photophores are covered over and lost in larger individuals.

Additional photophores begin appearing in some juveniles of 26 mm but are uncommon until after 28 mm. Unlike earlier photophores, they face ventrally and persist in adults. Earliest to appear are (1) a transversely barred thoracic organ (THO) located on the ventral body margin midway between the pectoral and pelvic fins, (2) two elliptical supraventral organs (SVO) located anterolateral to the bases of the ventral fins, and (3) two elliptical supraanal organs (SAO), lateral to the anal opening. Other adult photophores appear soon after and include a transversely barred midventral organ (MVO) located anteroventral to the SVO, the elliptical branchiostegal organs (BRO), the infracaudal organ (ICO) located on the ventral margin of the caudal peduncle, the pectoral organ (PO) located on the ventralmost ray of pectoral fins, and a longitudinally barred jugular organ (JO) located between the bases of the pectoral fins. All adult photophores are usually present by 50 mm.

Sagamichthys abei (Fig. 2)

Pigmentation The single larval specimen is nearly unpigmented. Most heavily pigmented areas are the eye, shoulder organ, subopercular photophore (SBO),

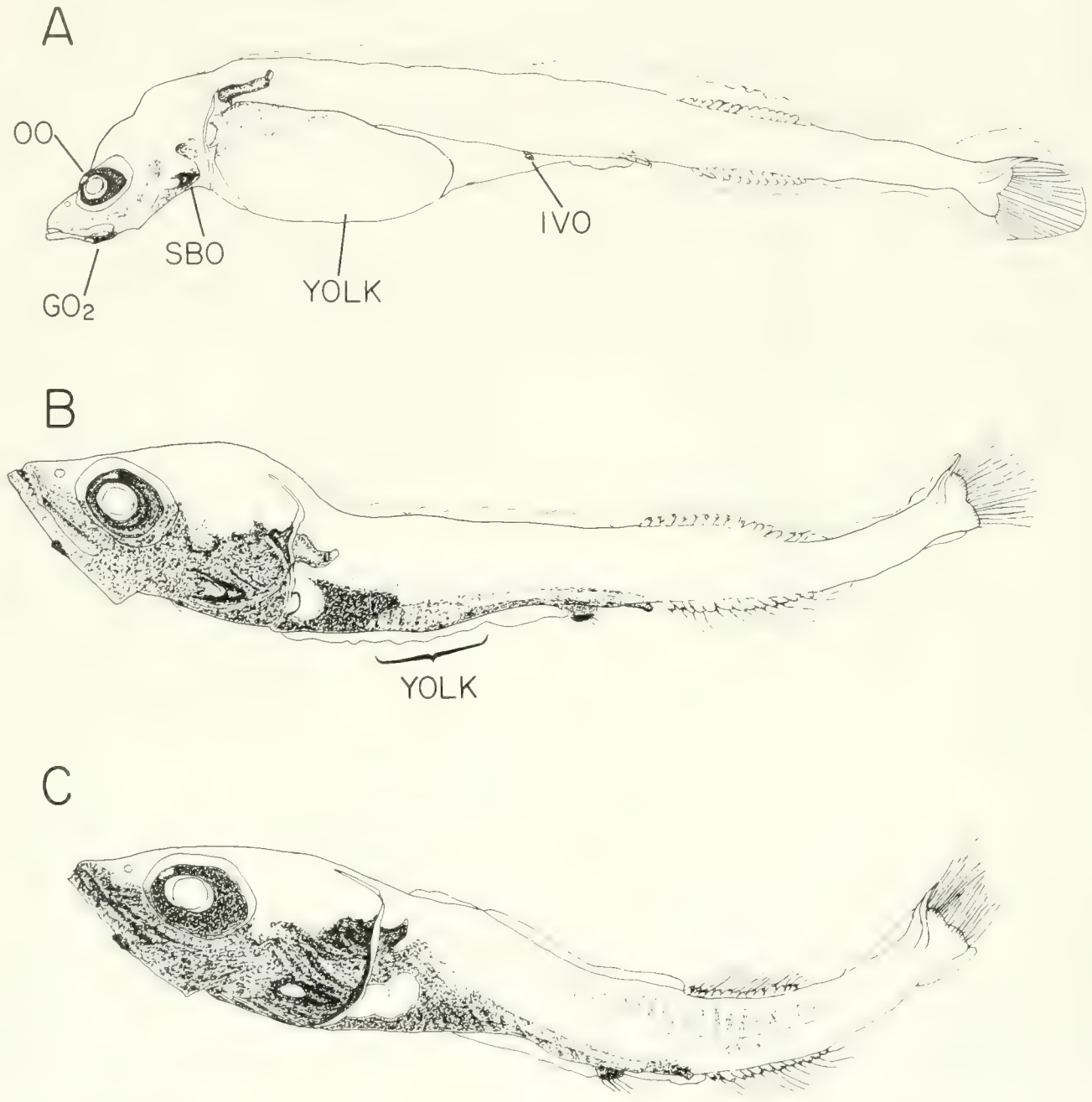

Figure 2

Camera lucida drawings of the young of *Sagamichthys abei*: (A) M13-1A, 16-mm larva; (B) SIO66-390, 14-mm transitional specimen; (C) M7 Sta 3, 16-mm juvenile. OO = orbital organ; GO_2 = posterior gular organ; SBO = subopercular organ; IVO = intraventral organ.

and posterior gular photophore (GO_2), with light pigmentation in the mouth, gill chamber, and on the dorsal region of the yolksac.

In the transitional specimen, the mouth, stomach cavity, and intestine are lined with black tissue. These blackened areas show through the translucent musculature, darkening the ventral half of the head and body anterior to the vent. Muscles between the anal and dorsal fins take on a bluish-black tinge, which spreads anteriorly and posteriorly from that area in larger individuals, with the area around the caudal peduncle darkening last. Among the more advanced transitional

Table 3

Measurements (in mm) and counts of *Sagamichthys abei*. SL = standard length, HL = head length, Hd = head depth at angular; asterisks = SIO.

	Sample no.												
	M13st1A	M4-st1	*66-390	*66-390	*66-422	*63-165	M7-st3	*66-371	*70-8	*65-439	*57-41	*75-472	*54-122
Lengths													
SL	16	16	14	14	14	13	16	16	16	17	17	18	20
HL	2.8	4.2	4.5	4.7	4.5	3.7	5.3	5.1	5.0	5.9	5.5	5.8	7.2
SL minus HL	13	12	9.5	9.3	9.5	9.3	11	11	11	11	12	12	13
Hd	1.5	2.0	2.3	2.3	2.1	2.1	2.7	2.3	2.6	2.4	2.4	2.3	3.2
Yolksac	4.0	4.2	2.5	2.5	3.2	2.6	0	0	0	0	0	0	0
Eye (long.)	0.92	1.1	1.1	0.92	1.0	0.76	1.7	1.8	1.3	1.7	1.3	1.6	2.2
Eye (vert.)	0.54	0.58	0.64	—	0.72	0.60	1.2	0.83	0.80	1.2	1.2	1.2	1.6
Maxilla	1.1	1.5	1.8	—	1.7	0.92	—	2.2	2.1	2.4	2.4	2.3	3.0
Counts													
Dorsal rays	0	16	16	14	13	13	14	16	14	16	15	16	15
Anal rays	0	14	13	14	13	12	14	15	13	15	14	14	14
Pectoral rays	0	0	3	0	3	0	5	—	5	7	4	7	5
Branchiostegals	0	8	8	8	8	8	8	8	8	8	8	8	8
Gill rakers	0	0+9	0+10	0+11	0+8	0+7	1+12	1+11	3+13	2+11	2+10	3+12	3+13
Pseudobranchiae	2	2	2	2	2	2	2	3	3	3	3	3	3
Dentition													
Vomerine	0	0	0	2	2	2	2	2	1	2	2	2	2
Palatine	0	1+0	0	1+1	1+0	1+1	1+1	1+1	0	1+1	1+1	1+1	1+0
Basihyal	0	1	3	3	1	1	4	1	4	7	4	6	5
Basibranchial	0	0	0	0	0	0	0	0	0	0	1	2	4
Dentary	0	3+?	3+5	7+?	8+?	5+5	?+14	10+8	15+11	17+?	14+15	17+?	12+?
Mid-dentary	0	0	0	0	0	0	0	0	3+2	4+?	2+3	2+?	?+3
Maxillary	0	0	0	0	0	0	4+6	—	9+6	10+?	9+?	11+14	12+?
Premaxillary	0	2+?	3+3	—	1+1	2+?	6+5	7+7	5+5	?+5	5+5	6+8	8+?

specimens, sparse epidermal pigment is found around the lower jaw, with a broken line at the midline between the anal and dorsal fins. This pigmentation spreads and intensifies in the juveniles, resulting in the blue-gray to black coloration.

Morphometrics A large yolk mass extends from the cleithrum to about halfway to the anus in the single larval specimen, which has a small head (headlength = 17% of SL) and mouth and undeveloped fins. Head length in transitional specimens nearly doubles to 26–33% of SL. Maxillary length increased from 7% SL to 9–13% SL during transition. Body length shortened or remained about the same (Table 3), as body length behind the head shortened. Head length and depth in transitional specimens are similar proportionately to adults, but the mouth is smaller than in adults and extends only to mideye, instead of behind the eye. Maxillary length is 9–13% SL during transition and 14–16% SL in adults. Eye length in the larva is proportionately similar to eye diameter in adults; however, eye depth is only half of the length in the former.

Head, mouth, and eye are proportionately largest in the 20–60 mm juveniles. Head length was mainly 35–38% of SL at this range (Table 4) but <30% of SL in individuals larger than 150 mm SL.

Fins All specimens have a flexed notochord and 19 principal caudal rays. Dorsal and anal fin rays are absent in the larval specimen, but pterygiophores of 11 anal and 13 dorsal rays are present. Counts of 13–16 dorsal, and 12–15 anal rays of the transitional specimens (Table 3) were nearly in the adult range of 16–18 dorsal and 14–16 anal finrays. Most juveniles over 20 mm SL had the adult counts. Pectoral fin rays are absent in specimens <18 mm. There were 0–7 pelvic rays at that length. Adult counts on all fins are found in juveniles >30 mm SL. There are 9–10 (usually 9) pelvic and 14–18 pectoral fin rays in the adult.

Branchial region Branchiostegal rays and gill rakers are absent in the larval specimen. Except for one individual with 7 rays, transitional specimens have the adult count of 8 branchiostegal rays. There are 8–11

Table 4

Summarized counts and morphometrics (% SL) of *Sagamichthys abei*. SL = standard length, HL = head length, Hd = head depth at angular.

			Dentition								% SL			
SL (mm)	Gill rakers	Pseudo-branchiae	Vomer-ine	Pala-tine	Pre-maxillary	Max-illary	Dentary	Mid-dentary	Basi-hyal	Basi-branchial	HL	Hd	Eye	Max-illary
Yolksac	0+0–11	2	0–2	0–1	0–3	0	3–8	0	0–3	0	18–33	9.3–16	6–8	7–13
16	1–3+11–13	2–3	2	1	5–7	6–9	10–15	0–3	0–4	0	31–33	14–16	8–15	13–14
17–20	2–4+11–13	2–3	2	1	5–9	7–14	12–18	1–4	4–8	0–8	32–43	14–21	8–11	13–18
21–25	3–5+13–15	3	2	1–3	8–9	7–19	12–25	1–3	4–8	2–9	34–35	15–18	9–10	14–16
26–30	4+15	4	3	2	13	19	17	5	9	10	35	16	10	16
31–35	4–5+15–16	4	2	2–5	9–11	17–26	15–19	3–5	6–12	6–9	34–36	16–22	8–10	14–15
36–40	6+16	4–5	2–5	2–3	10–14	25–28	16–22	6–9	5–9	4–6	30–39	17–20	9–11	16–18
41–45	6–7+17–18	5	2	2	11–12	28–29	28	6	3–7	6	32–36	8–16	7–9	15–19
46–50	6–7+15–16	6	2	2	11–12	34–35	22	6–7	5	6	34–38	18–20	9–10	17–20
51–55	7+19	7	2	2	17	41	26	10	7	14	41	22	9	20
56–60	7+16	6–7	2	2	13	37	23	9	2	9	35	20	8	18
61–65	7+16	7	2	2	13	40	24	10	4	5	36	19	8	17

gill rakers on the lower arch of the 1st gill arch in transitional specimens, but none on the upper arch. Epibranchial gill rakers were present in all juveniles examined (Table 4). The adult complement of 23–26 was present at about 50 mm.

An uninterrupted row of medial gill rakers is present on the 3d and 4th arches in 17-mm juveniles, but those on the 1st and 2d arches appear at 30–35 mm SL. There are 2 pseudobranchiae in the larva and transitional specimens. The number generally increased to 3 in juveniles of about 15 mm SL, and 6–7 in juveniles >45 mm SL.

Dentition The single larval specimen is toothless, but all transition specimens have teeth on the dentary, premaxillary, and basihyal, and, except for two individuals, on vomer and palatines as well (Table 3). Earliest appearances of maxillary, mid-dentary, and basibranchial teeth were in 16–17 mm juveniles. As in *H. latifrons*, there were more dentary than maxillary teeth in early stages; however, the number of maxillary teeth increased rapidly, becoming equal to that of the dentary by about 25 mm SL and more numerous after 35 mm (Table 4). Vomerine teeth numbered 2–5 and palatines 1–3 in the 16–50 mm SL range. In individuals 16 mm and larger, there were 3–12 teeth positioned around the perimeter of the basihyal, and 2–14 on the basibranchial. After a gradual increase, mid-dentary teeth numbered about 10 in individuals >50 mm SL. Mesopterygoid teeth appeared after 65 mm SL, and ectopterygoid teeth were found only in large adults.

Photophores The posterior gular organ (GO_2), subopercular organ (SBO), intraventral organ (IVO), and the orbital organ (OO) are the only photophores in individuals as large as 50 mm; they are covered over or lost in adults. The IVO photophore is located behind the yolksac (Fig. 2A). It becomes enclosed in a subconical, black pouch with a silvery, inner lining during the transitional period. The wider end of the pouch faces anteriorly and is covered by a transparent membrane. The photophore is located at the narrower, posterior end of the pouch, and is directed anteriorly. The other photophores are similarly housed in anteriorly facing, subconical pouches with a wider anterior opening and greater silvery surfaces.

Adult photophores face ventrally. Most begin appearing in juveniles. At 50–60 mm, the following organs begin to form: the jugular organ (JO) located between the bases of the pectoral fins; the thoracic organ (THO) behind the JO; the midventral organ (MVO) behind the THO and just before the pelvic fin bases; a pair of supraventral organs (SVO) just dorsal to the base of each pelvic fin; and the supra-anal organs (SAO) on both sides of the anus. The JO photophore first appears as one or more longitudinal bars (as in *H. latifrons*), but at about 65 mm begins to transform into a short transverse bar. Two more transverse bars, the THO and MVO, form behind the JO on the widely flattened ventral margin. Also appearing by 65 mm are several branchiostegal organs (BRO) on the branchiostegal rays, a postorbital organ (POO) just behind the eye, a pair of postanal organs (PAO) at about the middle of the anal fin, and an infracaudal organ (ICO) ventrally on the caudal peduncle. The anterior gular organ

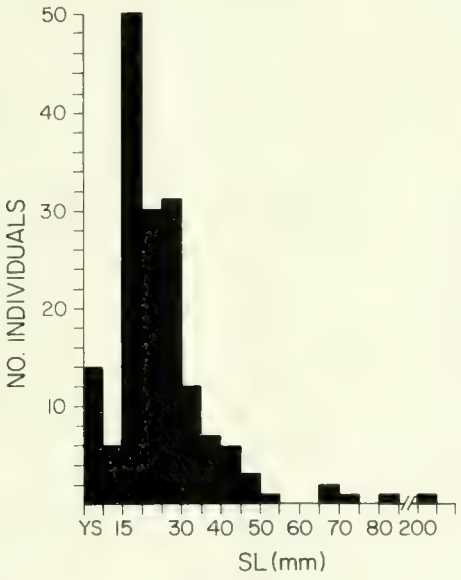

Figure 3
Length-frequency distribution of *Holtbyrnia latifrons* in SIO collections, 1950–73.

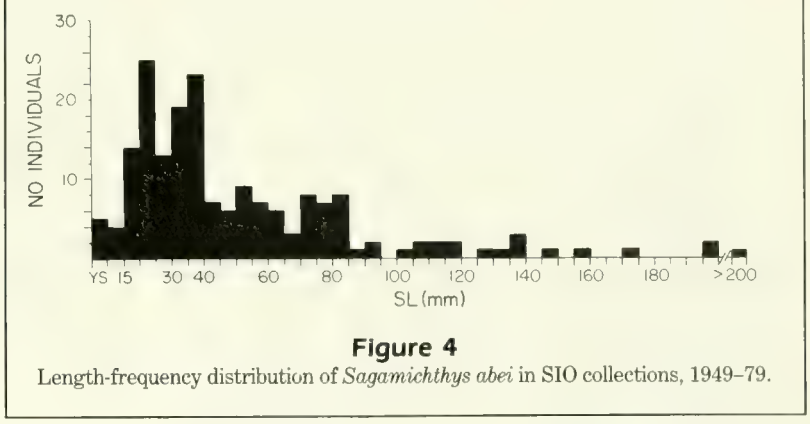

Figure 4
Length-frequency distribution of *Sagamichthys abei* in SIO collections, 1949–79.

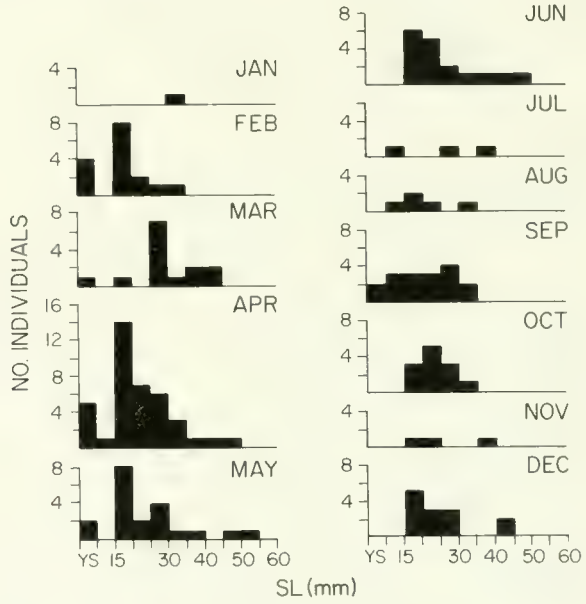

Figure 5
Length-frequency distribution of *Holtbyrnia latifrons* in SIO collections, 1950–73, presented by month of capture.

(GO_1), located just behind the mandibular symphysis, and the pectoral organ (PO) on the pectoral fins, appear by 75 mm. The anal organ (AO), located just before the anus, appears in large adults.

Remarks Some young specimens of *H. latifrons* and *S. abei* with nearly exhausted yolksacs retain characteristics of the earliest stages, i.e., fragile mouth, short head, and toothless mouth. Only the fin rays are relatively well developed. They appear to be starved in spite of the presence of yolk material and may indicate that they need to feed while the yolk is present. The severely underdeveloped head and mouth indicate that development either lagged from the very early stages or had regressed from a more advanced stage. These larvae were assumed to be atypical, and were not included in the larval description.

Distribution

In SIO samples, *H. latifrons* larger than 30 mm are rare and individuals >50 mm are nearly absent (Fig. 3); relatively small *H. latifrons* may avoid nets as large as a 3-m IKMT. Decline in size of *S. abei* in our samples is more gradual. The collection contains a number of individuals as large as 80 mm and a few even larger (Fig. 4). These results point to the inadequacy of nets as large as 3-m IKMT in sampling larger juveniles of both species.

The presence of individuals smaller than 20 mm during most of the year is interpreted as year-round spawning (Figs. 5, 6). These figures represent samples collected over many years pooled by month.

Depth distribution for both species is estimated to be 300–1000 m (Matsui and Rosenblatt 1987). On MLRG-SIO cruises, 63 opening-closing Leavitt net tows made in this depth zone collected 12 specimens of *H. latifrons* and 3 of *S. abei*. Fourteen net tows sampling shallower than 300 m and 30 tows sampling deeper than 1000 m on these cruises failed to catch

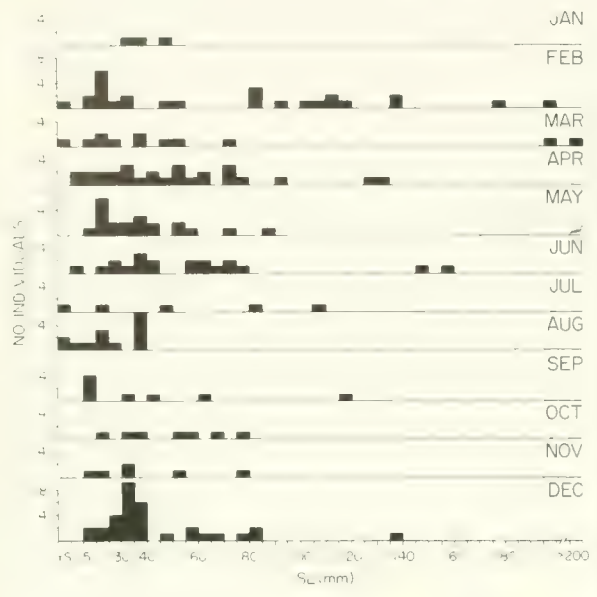

Figure 6
Length-frequency distribution of *Sagamichthys abei* in SIO collections, 1949–79, presented by month of capture.

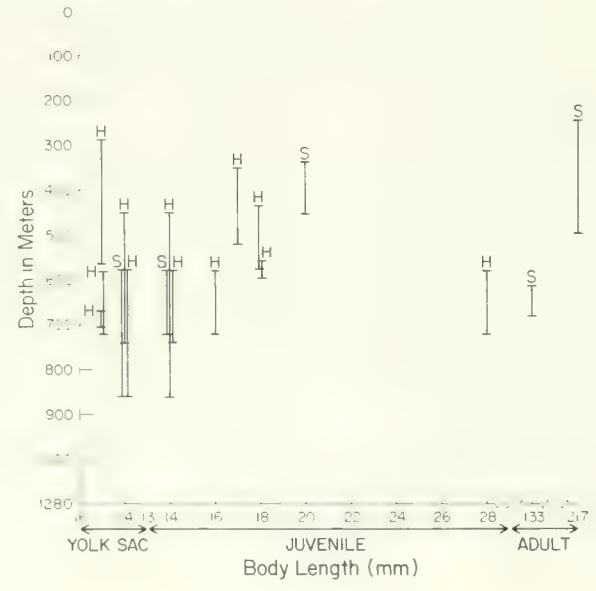

Figure 7
Sampling depths of opening-closing plankton net tows which captured *Holtbyrnia latifrons* (H) and *Sagamichthys abei* (S).

Table 5
Time and depth of capture of *Holtbyrnia latifrons* in opening-closing net tows. Asterisks = yolksac stage. Standard length (SL) in mm.

SL	Date	Time	Depth (m)
*14	2/09/72	0921–1021	450–740
*14	"	"	"
14	"	"	"
*14	4/09/72	1146–1355	580–860
14	"	"	"
*15	4/08/72	1639–1901	580–720
16	"	"	"
28	"	"	"
*15	2/02/71	1745–1845	669–706
18	"	"	558–595
17	12/20/71	1748–1848	350–520
18	2/02/71	2320–0025	433–573
*15	4/13/71	0013–0152	286–563

Table 6
Time and depth of capture of *Sagamichthys abei* in opening-closing nets. Standard length (SL) in mm.

SL	Date	Time	Depth (m)
20	2/09/72	0921–1021	333–450
14	4/08/72	1146–1355	580–860
133	11/04/69	1230–1300	615–680
15	4/08/72	1639–1901	580–720
213	3/28/70	2246–2350	250–500

either of these species. Samples of *H. latifrons* were from nets that had sampled depths of 290–860 m, and *S. abei* of 330–860 m (Fig. 7). All of these individuals were 20 mm and smaller, providing evidence that young stages occur over the entire depth range of the species. Large larval size and early appearance of presumed swimming and foraging capabilities, noted in this study, are apparent specializations for developing at these nutrient-poor depths.

Absence of day and night differences in depth of capture (Tables 5, 6) add to the previous evidence (Matsui and Rosenblatt 1987) suggesting the absence of diel migration in platytroctids. Hart (1973) and Fitch and Lavenberg (1968) mention the migration of young *S. abei* to within 200 m of the surface at night, but did not give the source of their information. However, records of platytroctids from depths 200 m and shallower are extremely rare and the single record from the Pacific Ocean may be an error (Matsui and Rosenblatt 1987).

Hydrographic data (Fig. 8) taken in an area where most Leavitt net tows were made show that samples represented in Figure 7 were taken below the thermocline at depths where the temperature range was ~4–8°C. CalCOFI (California Cooperative Oceanic

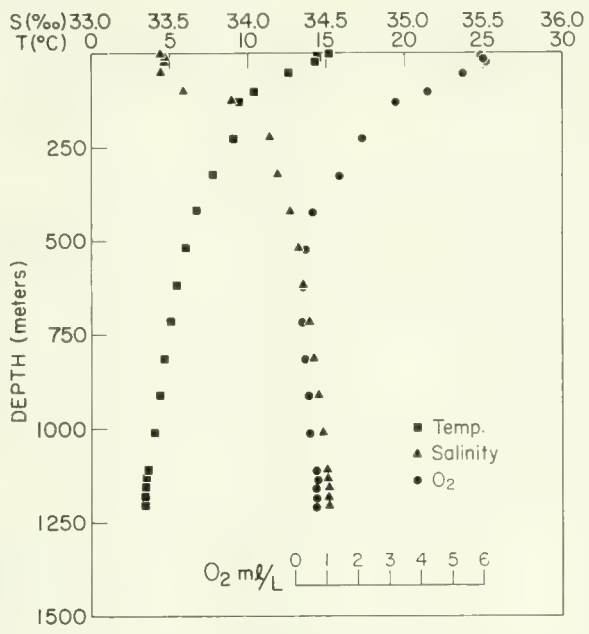

Figure 8

Temperature, oxygen, and salinity distribution at Station 7403G (32°32.4′N, 117°34.5′W), taken 27 March 1974 in the San Diego Trough.

Fisheries Investigation) station data from the area show seasonal changes in temperature below 300 m averaging less than 0.5°C (Lynn et al. 1982). Oxygen values of less than 1 mL/L occurred at these depths (Fig. 8). Gill filaments are highly developed (for platytroctids) in both species and are well adapted for this environment (Matsui and Rosenblatt 1987).

Acknowledgments

This study was supported by the Marine Life Research Program, the Scripps Institution of Oceanography's component of the California Cooperative Oceanic Fisheries Investigation.

I thank Dr. Richard Rosenblatt for loan of specimens from the SIO Fish Collection, and his staff for curatorial assistance. I am grateful for advice received from Dr. Geoffrey Moser, and for his comments on an earlier draft; and to Barbara Sumida MacCall for useful comments on illustrations of the larvae and juveniles. Other figures were prepared by the Marine Life Research Illustration department. I wish to thank Ron McConnaughey for his able assistance during the MLRG cruises, and other participants too numerous to be named here.

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Maturation, Spawning Seasonality, and Proximate Spawning Stimuli of Six Species of Tuna Baitfish in the Solomon Islands

David A. Milton
Stephen J.M. Blaber

CSIRO Division of Fisheries, Marine Laboratories
P.O. Box 120, Cleveland, Queensland 4163, Australia

Abstract.– Length-at-sexual-maturity and spawning periodicity of the tuna baitfish *Encrasicholina devisi*, *E. heterolobus*, *Spratelloides delicatulus*, *S. gracilis*, *S. lewisi*, and *Archamia zosterophora* were studied at two exploited fishing grounds and one unexploited site in the Solomon Islands. All species became sexually mature and capable of spawning at 70% of the largest size, except the apogonid *A. zosterophora* which matured at a larger size (80%). There was little site-related variability in length-at-first-spawning, although *S. lewisi* from Tulagi grew to a larger size and was larger than *S. lewisi* from other sites when it spawned for the first time. There was no evidence that length-at-first-spawning was affected by commercial baitfishing.

The timing and intensity of spawning of each species were extremely variable. All species spawned throughout the year, with one or two periods of more intense activity. The spawning peaks of the same species at different sites did not coincide, and no proximate stimuli correlated with spawning by any species at all sites. The timing of major spawning events was not random, nor did fish spawn as soon as they reached maturity. Spawning events at the three sites correlate with particular environmental conditions, especially moon phase and, less importantly, rainfall and temperature. These results are not consistent with the hypothesis that spawning is timed to maximize either local dispersal or the potential for larvae to find suitable food. Lack of clear proximate stimuli for spawning among the six species examined makes it difficult to predict the timing of major spawning events by these species.

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The pole-and-line fisheries for skipjack tuna *Katsuwonus pelamis* in the Pacific are dependent on adequate supplies of suitable bait. Engraulids (genus *Encrasicholina*) and dussumierids (genus *Spratelloides*) are the basis of the Solomon Islands tuna baitfishery, the largest in the region with catches of over 2000 t annually (Anon. 1988).

Knowledge of the reproductive biology of the main bait species may be important in developing management regimes to minimize the impact of the baitfishery on these species. Some aspects have been studied in the Solomon Islands (Evans and Nichols 1984) and elsewhere in the Pacific (Tester 1955; Tiews et al. 1971; Leary et al. 1975; Dalzell and Wankowski 1980; Conand 1985; Dalzell 1985, 1986, 1987ab; Lewis et al. 1983; McCarthy 1985; Clarke 1987) and in southeast Asia (Dharmamba 1960; Tham 1965; Luther 1979; Chen 1984, 1986). These studies suggest both genera spawn year-round, with periods of increased spawning during spring and summer (Leary et al. 1975, Tiews et al. 1971, Luther 1979) or with the change of monsoon (Dalzell and Wankowski 1980, Dalzell 1987b) or periods of high zooplankton production (Sitthichockpan 1972). However, timing of peak spawning is variable, both temporally (e.g., Dalzell 1987b) and between regions.

There have been several reviews (e.g., Scott 1979, Lam 1983, Bye 1984) of the importance of various cues which stimulate gonadal development and cause fish to spawn (proximate factors). Among temperate species, temperature and light are the most common cues (Scott 1979, Bye 1984). Other cues, such as food supply, moon phase, and rainfall, have also been suggested as important for spawning by tropical marine fishes (Johannes 1978, Lam 1983, Walsh 1987). However, the proximate stimuli that arouse increased spawning activity among baitfish remain obscure. Tester (1955) found that variations in egg production by *Encrasicholina purpureus* in Hawaii could not be adequately explained by temperature, salinity, or moon phase. Similarly, Muller (1976) showed that fluctuations in salinity and zooplankton biomass accounted for only 30% of the variation in egg production of *E. heterolobus* at Palau. Such poor correlations suggest that spawning may be random, or fish may begin to spawn as soon as they are physiologically capable of doing so.

The length at which *Encrasicholina* and *Spratelloides* become sexually mature appears to be variable both between and within countries of the southwestern Pacific (Dalzell and Wankowski 1980, Conand 1985, Dalzell 1985, McCarthy 1985, Dalzell 1987ab, Wright 1989), and these fish may adjust their life-history parameters to changes in their demography

or environment (Stearns and Crandall 1984). Such variability could have important implications for the baitfishing industry. Juveniles could be caught before they have had a chance to spawn, because the liftnets used in the baitfishery are not size-selective and catch all sizes of *Encrasicholina* and *Spratelloides* (see Evans and Nichols 1984).

The aims of this study were, first, to examine the length at maturity and the spawning seasonality of the six most abundant baitfish species (*Encrasicholina devisi*, *E. heterolobus*, *Spratelloides delicatulus*, *S. lewisi*, *S. gracilis*, and the apogonid *Archamia zosterophora*); secondly, to determine whether spawning is random or correlated with environmental cycles; and, thirdly, to assess the effects, if any, of the commercial fishery on these reproductive parameters.

Table 1
Criteria used for staging female gonads of baitfish.

Stage	Histology
(1) Immature	Oogonia present
(2) Developing/resting	Previtellogenic oocytes
(3) Maturing	Yolk precursor stage; some non-staining yolk
(4) Ripe	Non-staining yolk; developed chorion
(5) Running ripe	Homogeneous red-staining yolk; oocytes hydrated; development complete
(6) Spent	Atresion of ripe oocytes plus previtellogenic oocytes; presence of post-vitellogenic follicles

Methods and materials

Sampling

Samples of six species of baitfish were collected from three sites each month for two years. Fish from commercial bait catches came from Munda and Tulagi, and fish from an unexploited control site came from Vona Vona, Solomon Islands. Sites and sampling methods are described in Milton et al (1990). Samples were usually collected between 2100 and 2200 hours. Two sites, Munda and Vona Vona, were in enclosed coral reef lagoons with little water movement and were approximately 20 km apart. The other site, Tulagi, consisted of a series of protected bays which opened into a narrow channel between two islands and was located over 300 km southeast of the other sites. Each month a random sample of over 100 fish of each species from each site was preserved in 4% formaldehyde and taken to the laboratory for analysis. On each sampling occasion, the water temperature, cloud cover, moon phase, and wind speed and direction were recorded. At least two 5-minute horizontal plankton tows ($\sim 100\,m^3$) were made with a 250-μmm mesh net (0.5 m diameter) 1 hour prior to fish collection. The daily rainfall at a village adjacent to each site was recorded throughout the study.

Laboratory analyses

Fish were measured (standard length (SL) ± 0.5 mm) and weighed (± 0.001 g) and the gonads were removed and weighed (± 0.001 g). The gonads of up to 10 females of each species and of any other females with enlarged oocytes were randomly subsampled from each site sample each month. Gonads were embedded in paraffin wax, sectioned at 9μm, and stained with Ehrlich's haemotoxylin and eosin (McManus and Mowry 1964). Gonad maturation stages were defined following Cyrus and Blaber (1984) and Hunter and Goldberg (1980). Each gonad was staged, based on the relative numbers of cells at each developmental stage (Young et al. 1987; Table 1), and the presence of any postovulatory follicles was noted. Gonosomatic indices (GSI) were calculated as the ratio of wet gonad weight to somatic weight (total weight minus gonad weight) expressed as a percentage.

Size-at-sexual-maturity was determined from the length at which a fish developed ripe eggs (Table 1: stage 4). Among fish that were only examined macroscopically, the criterion for sexual maturity was a gonosomatic index greater than the minimum GSI of fish that were shown histologically to have ripe eggs.

Fish examined histologically were considered to be in spawning condition if more than 85% of the eggs were fully hydrated, running-ripe (Table 1: late stage 5). The mean GSI ± 2 standard errors of these fish was calculated for each species at each site. The GSI value of the lower 95% confidence limit of the mean GSI of spawning fish was used as the indicator of spawning among fish examined macroscopically. The proportion in spawning condition in each sample was then calculated from the fraction of the sample (examined both histologically and macroscopically) with a GSI greater than this value. This criterion was used, as it was a conservative estimate of the real proportion spawning.

Plankton samples were split in half with a Folsom plankton splitter and one fraction was dried to a constant mass to provide an estimate of relative zooplankton biomass. The other fraction was sorted and the number of *Encrasicholina* eggs and larvae (Delsman 1931), the number of other eggs, larvae, and potential

prey (from those found by Milton et al. 1990) were counted. *Spratelloides* eggs are demersal (Leis and Trnski 1989) so were not sampled by this method.

Data analyses

The proportion of each 1 mm length-class that were sexually mature was compared between sites. The normal approximation to the binomial distribution was used to estimate the 95% confidence limits of the proportion mature in any length-class. Confidence limits of the estimated proportion of the mature population spawning each month were calculated in a similar way.

To assess whether the timing of spawning was random, we calculated the proportion of the population spawning from the fraction of the entire sample of each species at each site during the study. This proportion was then compared with the proportion spawning each month. Monthly proportions greater than the 95% confidence limits to the normal approximation to a binomial distribution were scored as a plus sign. A non-parametric runs test (Sokal and Rohlf 1981) was used to test whether the distribution of plus signs was random.

The relationship between the proportion of fish in each monthly sample (of each species at each site) that were longer than the mean adult length at that site, and the proportion in that sample that were spawning, was examined using linear regression. A significant positive relationship between these proportions was used to assess whether fish spawned as soon as they were physiologically capable of doing so.

The relationships between possible proximate stimuli and the proportion spawning were compared by stepwise regression analysis. Variables that improved the fit were added to the model until the best three-variable model was obtained or the most significant fit was found. The proportion of each sample of each species in spawning condition was transformed by its arcsine square-root to reduce possible bias due to an excess of low values (Sokal and Rohlf 1981). The following 11 variables were compared for each species at each site: (1) sea-surface temperature, (2,3) prey biomass and density, (4) moon phase, (5) tide range, (6) cloud cover, (7) wind speed, and (8–11) rainfall between samples. Previous studies of spawning by these species (Dalzell 1985, 1987b) and other tropical inshore fishes (e.g., Johannes 1978, Walsh 1987) suggested that these variables may be important cues for these species. Initially, salinity and current speed were also measured, but as they varied little, they were not included in the analysis.

The variable moon phase was calculated by fitting a curve of the form $y = \sin(2\pi x) + \cos(2\pi x)$ where x = number of days since the last full moon prior to the start of sampling divided by 29.5 (days in a lunar month). This variable has higher values about the new and full moon. Rainfall data were regressed in several ways to assess the influence they may have on baitfish spawning: total rainfall since previous sample (usually 1 month)(Total); number of days since rain (Days); number of days since rain >25 mm (Days 25 mm); and number of days of rain since previous sample (Rain). Rainfall, cloud cover, and wind variables were transformed by their square root to normalize skewed values. Except for moon phase, positive relationships between the proportion of each species spawning and proximate variables are indicative of greater spawning activity at higher values.

To assess whether all variables were independent, proximate variables were correlated with one another. Principal component analysis (Sokal and Rohlf 1981) was also used to help identify variables that covaried within and between sites. A subset of proximate variables that behaved independently was identified and analysed separately. Where a potential stimulus had been measured in several ways (e.g., rainfall), the most biologically appropriate was chosen.

Results

Physical environment

The mean sea-surface temperature and monthly rainfall at each site varied seasonally during the sampling period (Figs. 1–3). The temperature ranged from 27.5° to 32.5°C at all sites, with lower temperatures during the dry season (May–September). Temperatures were lower in 1987 than 1988 at all sites. Rainfall occurred in all months at all sites. The amount of rainfall and its monthly distribution pattern were similar at the two closest sites, Munda and Vona Vona (r^2 0.48, $P<$ 0.05), but Tulagi had a higher rainfall and different pattern of distribution.

Maturation

A total of 1159 fish of six baitfish species from the three sites were examined histologically, including over 200 of each of the four most abundant species: *Encrasicholina devisi*, *E. heterolobus*, *Spratelloides delicatulus*, and *S. lewisi*.

Encrasicholina Histological examination of ripe ovaries of *E. devisi* and *E. heterolobus* showed that almost all oocytes were in the most advanced stage of development, with a few at the yolk precursor stage (Table 1) or less developed. Although many females (~15%) of those examined had hydrated eggs, no post-vitellogenic follicles or spent fish (Stage 6) were observed.

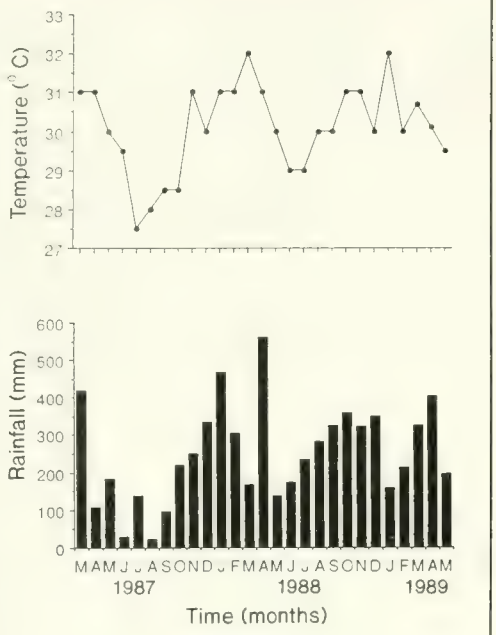

Figure 1
Mean monthly sea temperature and rainfall at Munda, Solomon Is., March 1987–May 1989.

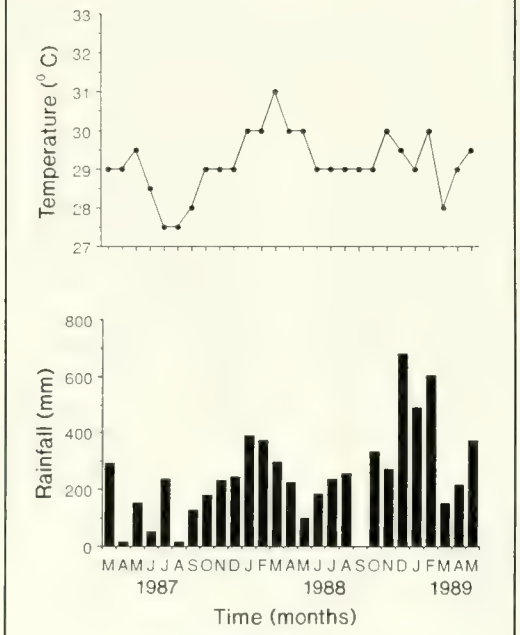

Figure 3
Mean monthly sea temperature and rainfall at Tulagi, Solomon Is., March 1987–May 1989.

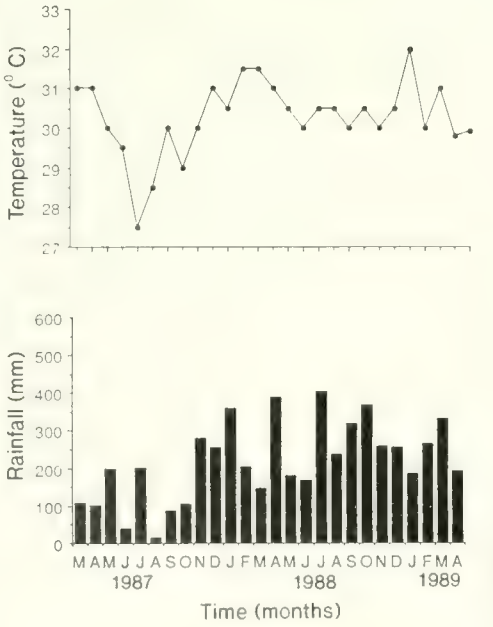

Figure 2
Mean monthly sea temperature and rainfall at Vona Vona, Solomon Is., March 1987–May 1989.

In both *Encrasicholina* species, fish with a GSI greater than 2% (Table 2) were sexually mature. The size at maturation of *E. devisi* was similar at all sites with 50% of the fish being sexually mature at 44–45 mm (Fig. 4a). At Munda and Vona Vona, fish beyond this length were capable of spawning, but at Tulagi the smallest *E. devisi* in spawning condition was 52 mm (Table 2). Sexual maturity in *E. heterolobus* was reached at approximately 43 mm at Munda and Vona Vona (Fig. 4b) and 45 mm at Tulagi. Hydrated eggs were not observed in *E. heterolobus* less than 50 mm, except at Munda where the smallest potential spawner was 45 mm (Table 2).

Spratelloides The three *Spratelloides* species at the three sites were mature at similar lengths. *Spratelloides gracilis* and *S. lewisi* were sexually mature and had hydrated eggs at 35 mm (Table 2, Fig. 4c), except at Tulagi where the smallest *S. lewisi* with running ripe eggs was 40 mm. *Spratelloides delicatulus* reached sexual maturity at 37 mm (Fig. 4d), and running-ripe eggs were found in fish beyond this length. However, their length-at-maturity was not significantly different from the other *Spratelloides* species ($P>0.1$). For all species, a gonosomatic index of over 2% correlated with fish having ripe eggs (stage 4) in the ovary. Most oocytes in the ovaries of females of these species were at a

Table 2

Minimum gonosomatic index (GSI) values used as criteria to estimate proportion of sexually mature fish (stage 3) and proportion of fish spawning (late stage 5) at each site, and minimum size (SL, mm) of fish in spawning condition (based on values obtained from fish examined histologically). *N* = sample size.

		Sexual maturity		Spawning		
Species	Site	GSI (%)	*N*	GSI (%)	Length	*N*
Archamia zosterophora	All	2.5	57	3.8	37	23
Encrasicholina devisi	Munda	2.0	86	9.0	45	39
	Vona Vona	1.8	80	7.0	45	41
	Tulagi	1.8	58	5.7	52	11
Encrasicholina heterolobus	Munda	2.0	134	8.5	45	26
	Vona Vona	1.9	135	8.8	50	24
	Tulagi	1.6	84	10.0	51	31
Spratelloides delicatulus	Munda	2.0	60	5.7	37	34
	Vona Vona	1.0	35	5.9	37	23
	Tulagi	1.2	43	5.5	38	25
Spratelloides lewisi	Munda	1.5	235	13.3	35	210
	Vona Vona	2.8	107	11.2	35	90
	Tulagi	1.0	24	12.5	40	10
Spratelloides gracilis	All	2.0	12	11.9	35	6

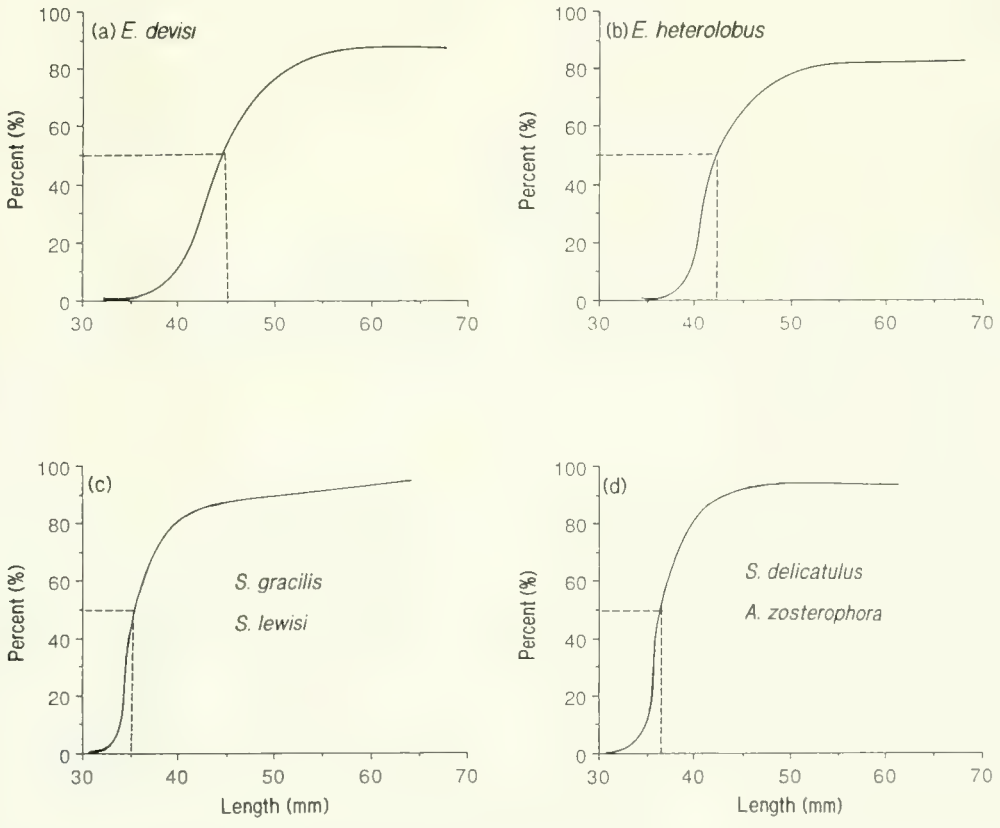

Figure 4

Logistic curves of best fit which describe the change in proportion of ripe eggs (stage 4) in the ovaries of six species of baitfish with increasing fish length.

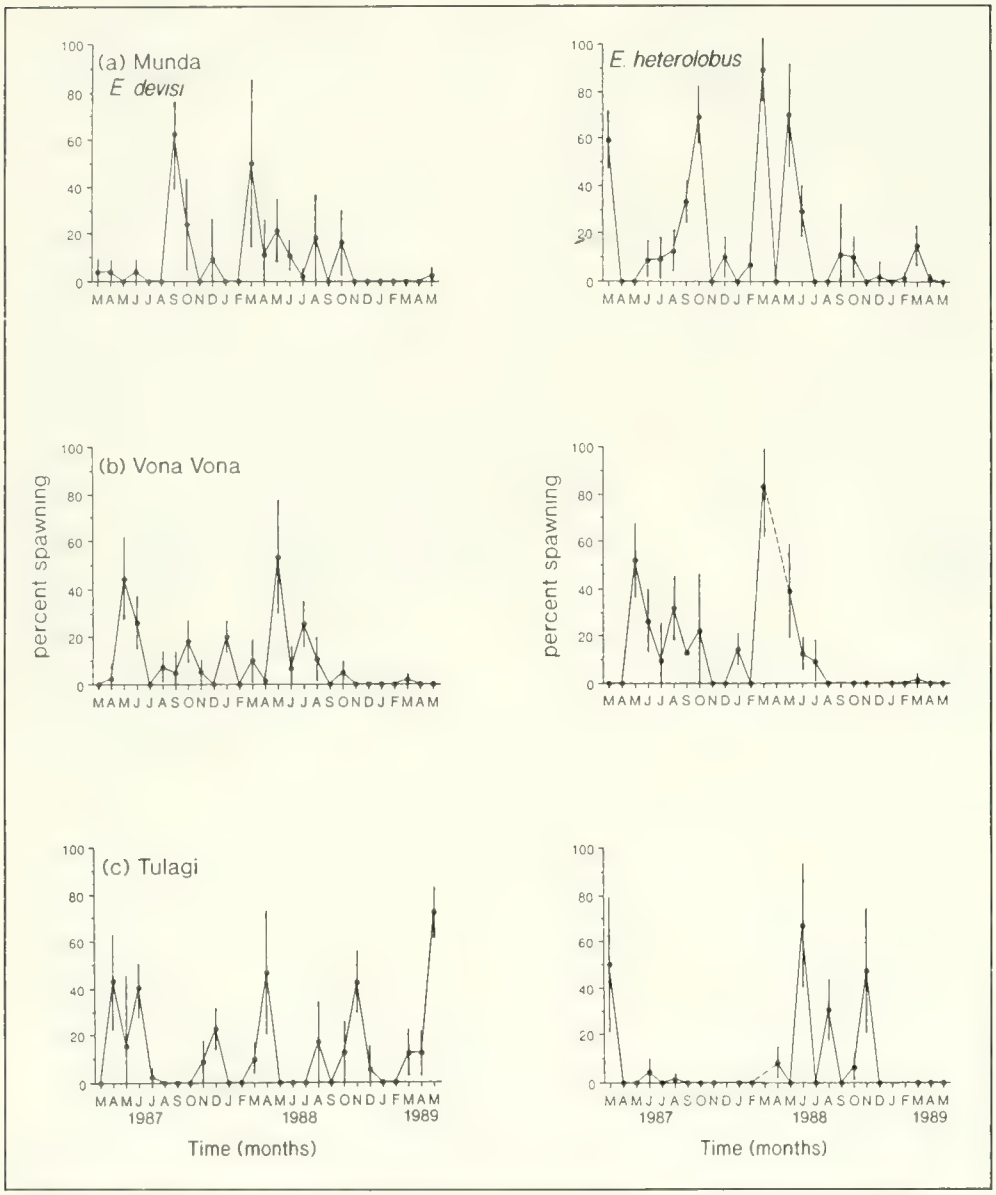

Figure 5
Monthly variation in proportion (± 95% confidence limits) of female *Encrasicholina devisi* and *E. heterolobus* spawning at three sites in the Solomon Islands, March 1987–May 1989.

similar stage of development. Fish with spent ovaries (Stage 6) were observed but were rare (<1%).

Archamia zosterophora This species matured at 37 mm and was capable of spawning at this length (Table 2, Fig. 4d). A gonosomatic index value greater than 2.5% corresponded with sexual maturity (Table 2).

Spawning seasons

All non-parametric tests showed a significant deviation from random spawning for all species at all sites ($P<0.05$). The distribution of deviations (plus signs) was either clumped or regular. For no species at any site were there significant positive correlations between the proportion of larger fish and the proportion spawning ($P>0.05$).

Encrasicholina Spawning activity by the two *Encrasicholina* species showed both seasonal and interannual variation (Fig. 5). Both species had one or two major peaks in spawning each year. However, the pattern was different each year. Both species had a major peak in spawning activity early in the year (March–May) during 1987 and 1988, except for *E. devisi* at Munda in 1987 when most fish spawned later (Sept.–Oct.). The peak spawning was usually followed by several months when a small proportion of the population was spawning. Patterns of spawning at Munda and Vona Vona were more similar than at Tulagi. *Encrasicholina*

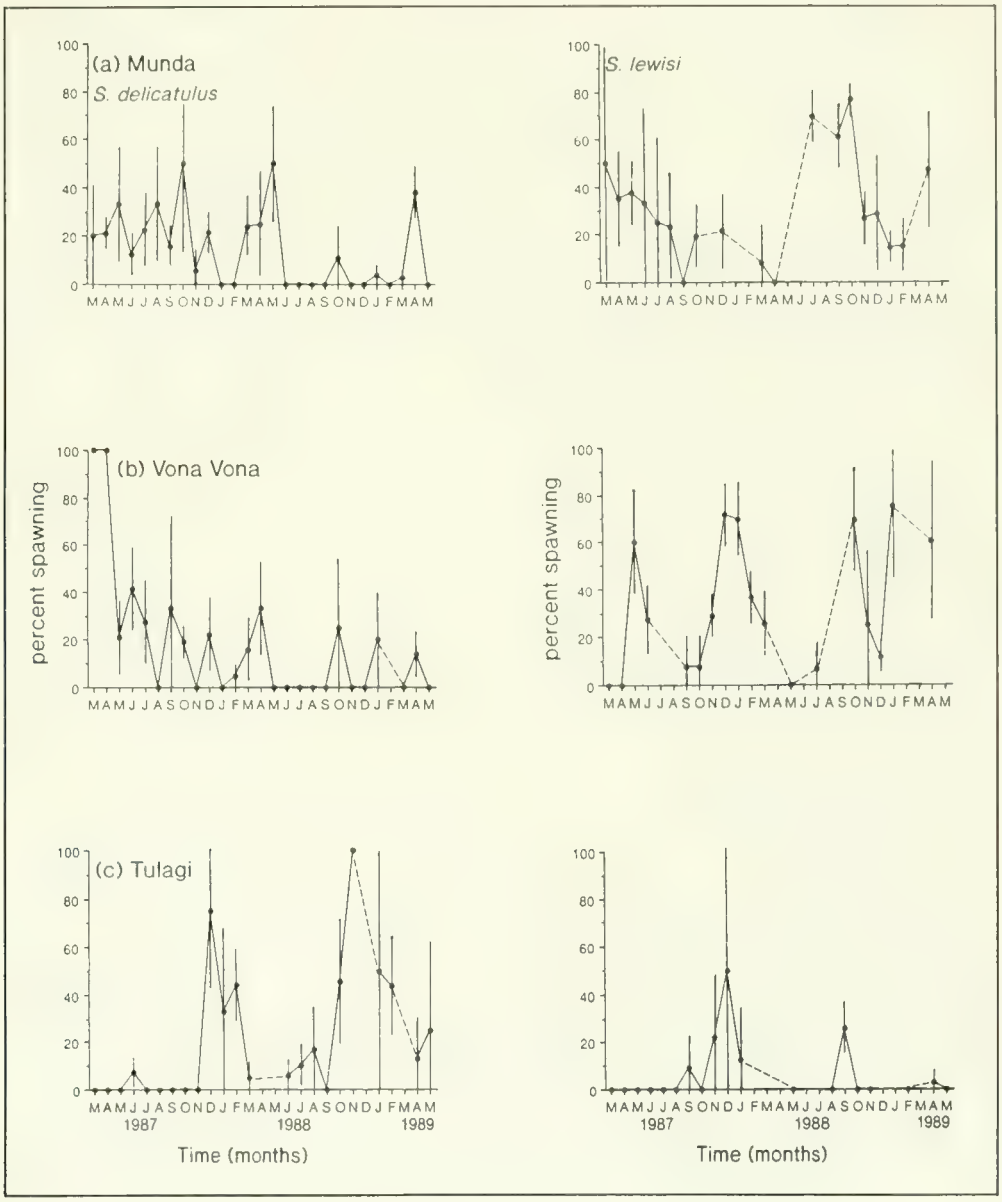

Figure 6
Monthly variation in proportion (± 95% confidence limits) of female *Spratelloides delicatulus* and *S. lewisi* spawning at three sites in the Solomon Islands, March 1987–May 1989.

heterolobus also had fewer, smaller peaks in spawning activity during most of 1987 at Tulagi and at all sites during the first five months of 1989. *Encrasicholina devisi* in Munda and Vona Vona did not have a March–May spawning peak in 1989.

Spratelloides Two *Spratelloides* species also showed inter- and intraspecific differences in spawning activity between sites and between years (Fig. 6). *Spratelloides delicatulus* spawned continuously during 1987 at both Munda and Vona Vona, but the proportion spawning declined in the next 17 months. At Tulagi, the pattern was reversed, with less spawning during 1987 than in 1988–89 when there was a single major protracted spawning season from December to March (Fig. 6c). *Spratelloides lewisi* showed seasonal spawning activity at all sites. Fish from Vona Vona and Tulagi had a similar pattern during 1987–88, with increased spawning activity from October to May. However, the proportion spawning at Tulagi (50%) was much lower. The spawning activity of *S. lewisi* at Munda showed no seasonal increase during 1987, although during 1988 a higher proportion was spawning during the middle of the year (Fig. 6).

Too few *S. gracilis* and *A. zosterophora* could be obtained to determine their spawning seasons. However, a proportion of the fish sampled of both species was in spawning condition for several months of the year (Fig. 7). *Archamia zosterophora* data from Munda showed that some spawning activity occurred through-

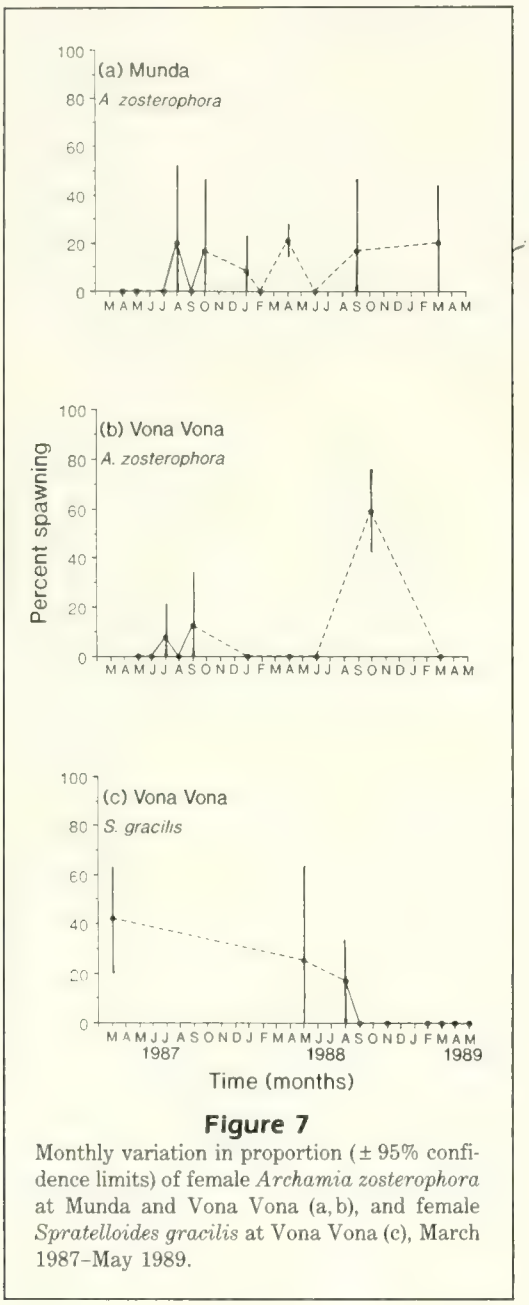

Figure 7

Monthly variation in proportion (± 95% confidence limits) of female *Archamia zosterophora* at Munda and Vona Vona (a, b), and female *Spratelloides gracilis* at Vona Vona (c), March 1987–May 1989.

out the year. At Vona Vona, however, there was a peak in spawning activity in samples taken in October 1988. The spawning data for *S. gracilis* are consistent with data for other *Spratelloides* at Vona Vona, with a decline in spawning activity during late 1988 and 1989 (Fig. 7).

Eggs and larvae *Encrasicholina* eggs were present in the zooplankton at each site most months of the sampling period (Fig. 8). The abundance of eggs did not vary greatly at each site during the period, although the samples from Vona Vona had fewer eggs than the other sites. Overall, the mean *Encrasicholina* egg density for the entire sampling period varied from $0.08 \pm 0.03/m^3$ at Vona Vona to 0.43 ± 0.10 at Munda. The overall mean teleost egg density was also lower at Vona Vona ($1.34 \pm 0.21/m^3$) and highest at Munda ($4.98 \pm /m^3$). *Encrasicholina* egg density did not correlate with total egg density at any site ($P>0.3$) or with the proportion of spawning *E. devisi* or *E. heterolobus* ($P>0.5$). No *Spratelloides* larvae were found, although apogonid larvae were present but could not be identified to species.

The density of *Encrasicholina* larvae followed a similar pattern at all sites (Fig. 8): larvae were present in most months, increasing every three or four months. In contrast to egg densities, *Encrasicholina* larvae reached higher densities at Vona Vona ($0.05 \pm 0.01/m^3$) than at Munda ($0.03 \pm 0.006/m^3$). Other fish larvae were also in higher densities at Vona Vona (1.15 ± 0.27) than at the other sites (Munda 0.93 ± 0.26 and Tulagi 0.60 ± 0.22). The density of *Encrasicholina* larvae was significantly correlated with the density of other fish larvae at Munda (r^2 0.62, $P<0.05$), but not at other sites.

Proximate spawning stimuli

To assess the independence of the 11 proximate stimuli, all variables were correlated with one another (Table 3). At all sites, most measures of rainfall were significantly correlated ($P<0.05$). Total rainfall was negatively correlated with moon phase at Vona Vona and Tulagi, and with zooplankton biomass at Tulagi. Cloud cover was correlated with total rain and days of rain at Tulagi ($P<0.05$). Zooplankton biomass and density were correlated at Munda and Tulagi. However, there were no consistent correlations at all sites between non-rainfall variables (Table 3).

Principal component analysis was also performed separately on the proximate variables from each site. Rainfall variables at each site had loadings on the first three factors that were similar in magnitude and direction. Zooplankton density and biomass also covaried at each site. Temperature, moon phase, tide, and wind had loadings that varied independently for the first three factors at each site. These variables, zooplankton density, and the number of days of rain (which covaried least with other rainfall variables) were used in a separate stepwise regression analysis.

Encrasicholina Analysis of the relationships between all 11 environmental parameters and the proportion of each sample spawning showed no consistent pattern for either species of *Encrasicholina* (Table 4). At Munda, spawning of *E. devisi* positively correlated

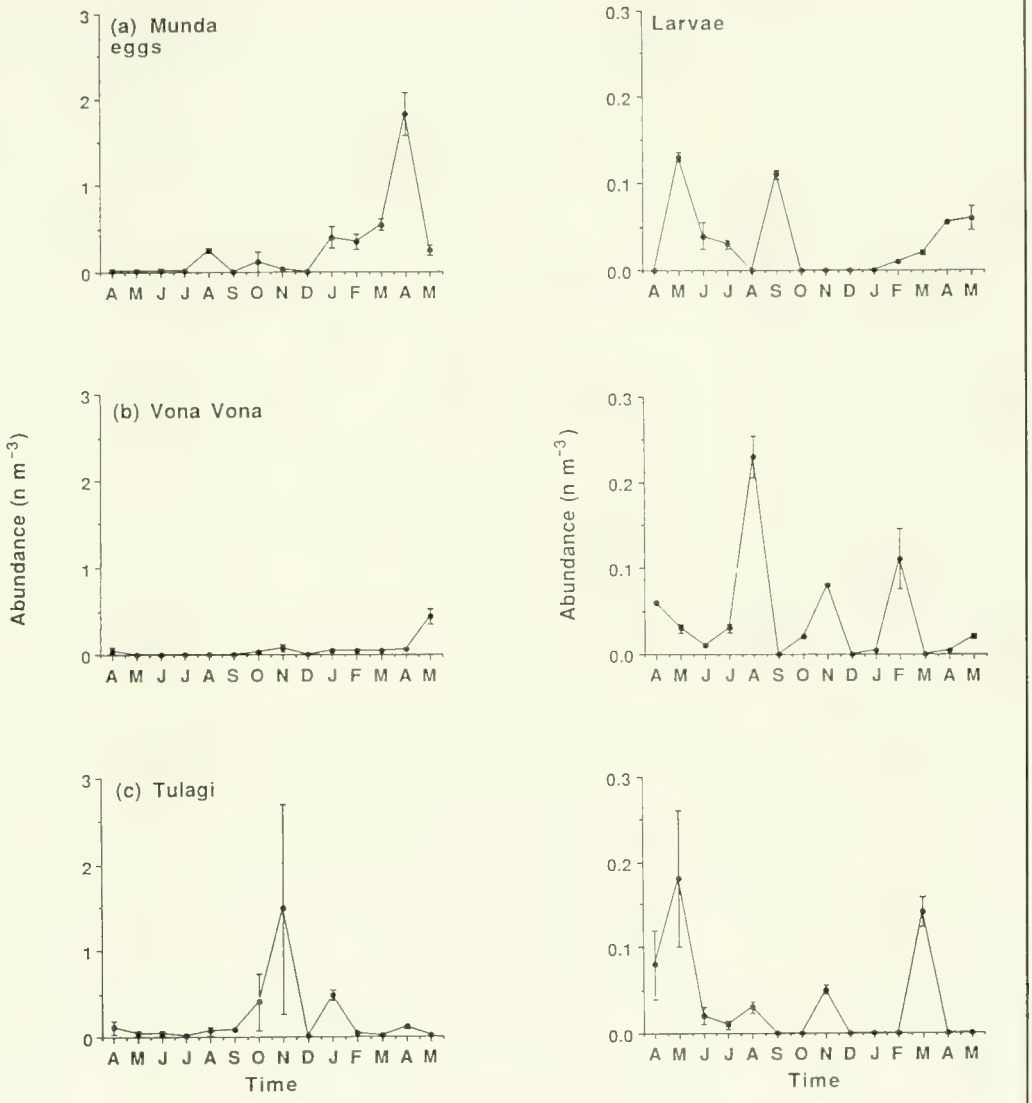

Figure 8

Variation in monthly abundance of *Encrasicholina* eggs and larvae (± range) at three sites in the Solomon Islands, April 1988–May 1989.

with wind and time since rain. At Vona Vona there was a negative correlation with wind strength and positive correlation with zooplankton biomass and tide range. Spawning at Tulagi correlated most strongly with time since heavy rainfall (>25 mm), temperature, and zooplankton biomass (Table 4). When all data were included, time since heavy rain was the only significant correlate.

Stepwise regression analysis of the six independent proximate stimuli (Table 5) showed a much poorer fit. The only site that showed a significant relationship was Vona Vona, where full moon, greater tidal range, and low wind accounted for 40% of the variation in spawning of *E. devisi*. Although not significant, days of rain had a similar coefficient in the equations of best fit at both Munda and Tulagi (Table 5), which suggests that rainfall had a similar effect on spawning at these sites.

The significant proximate stimuli for *E. heterolobus* differed between sites (Table 4). The best fit was obtained at Vona Vona (r^2 0.44, $P<0.01$) where greater spawning occurred when cloud cover was low and moon phase approached full. Spawning was negatively related to total rainfall and days since rain at Munda (r^2 0.3, $P<0.05$), and there was a negative

Table 3

Correlations between independent environmental variables. *$P<0.05$. See "Data analyses" section for explanation of variables.

Variable	Temp.	Biomass	Density	Moon phase	Tide range	Cloud cover	Wind speed	Rain* Total	Rain* Days	Rain* Days 25mm	Rain* Rain
Munda											
Temperature	x	−0.02	−0.12	−0.32	−0.20	0.41	0.18	0.46*	0.04	−0.19	0.37
Biomass		x	0.73*	−0.21	−0.08	0.21	−0.38	0.08	−0.36	0.00	0.30
Density			x	0.05	0.23	0.29	−0.23	−0.03	−0.22	0.05	−0.01
Moon phase				x	0.06	0.01	0.50*	−0.29	0.3	0.51*	−0.29
Tide range					x	−0.07	0.07	−0.09	0.47*	0.12	−0.05
Cloud cover						x	0.25	0.30	0.01	0.11	0.17
Wind speed							x	0.16	0.33	0.23	−0.11
Total*								x	−0.21	−0.62*	0.69*
Days									x	0.52*	−0.31
Days 25mm										x	−0.54*
Rain											x
Vona Vona											
Temperature	x	−0.05	−0.46*	−0.25	0.08	0.38	0.06	0.25	−0.19	0.10	0.24
Biomass		x	0.31	−0.03	−0.32	0.21	0.39	−0.09	−0.15	−0.41	0.08
Density			x	0.19	−0.27	−0.15	0.26	−0.19	−0.03	−0.25	0.04
Moon phase				x	0.08	−0.29	−0.09	−0.55*	0.26	0.42*	−0.36
Tide range					x	−0.05	−0.34	−0.30	0.28	0.46*	−0.34
Cloud cover						x	0.49*	0.10	−0.21	0.03	0.25
Wind speed							x	0.16	−0.06	−0.28	0.12
Total*								x	−0.49*	−0.56*	0.62*
Days									x	0.33	−0.83*
Days 25mm										x	−0.44*
Rain											x
Tulagi											
Temperature	x	−0.22	−0.20	−0.22	−0.33	0.10	−0.11	0.33	−0.40	−0.21	0.11
Biomass		x	0.70*	0.41*	0.24	−0.33	−0.15	−0.45*	0.14	0.09	−0.44*
Density			x	0.19	0.22	−0.45*	−0.45*	−0.40*	0.49	−0.05	−0.52*
Moon phase				x	0.22	−0.38	0.04	−0.51*	−0.00	0.10	−0.35
Tide range					x	−0.18	−0.19	−0.18	0.28	−0.13	−0.26
Cloud cover						x	0.39	0.52*	−0.33	−0.25	0.72*
Wind speed							x	0.06	−0.24	0.10	0.21
Total*								x	−0.36	−0.42*	0.67*
Days									x	0.15	−0.44*
Days 25mm										x	−0.29
Rain											x

*Total = Total rainfall since previous sample
Days = No. days since rain
Days 25mm = No. days since rain >25mm
Rain = No. days of rain since previous sample.

relationship with tide range at Tulagi. Overall, the most significant variable was total rainfall. The results of the regression analysis of the independent stimuli (Table 5) were similar, except at Vona Vona where a four-variable model including zooplankton density, wind, and days of rain gave the best fit.

Spratelloides For *S. delicatulus*, moon phase was highly correlated with spawning and accounted for at least 26% of the variation in spawning periodicity at all sites (Table 4). Increased cloud cover and reduced tidal range were also correlated with spawning at Vona Vona and Tulagi. However, when data from all sites were combined, the most significant correlates were

Table 4

Stepwise multiple regresssion of best fit of 11 proximate variables related to the proportion of each species spawning at each site. Maximum number of variables allowed was three. Negative sign preceding a variable indicates negative correlation; r_p^2 = partial correlation coefficient, r^2 = overall correlation coefficient, P = significance level, N = sample size.

Species	Site		Environmental parameter	r_p^2	r^2	P	N
Encrasicholina devisi	Munda		Days since 25 mm rain	0.16	0.35	<0.05	22
		—	Days since rain	0.10			
			Wind speed	0.09			
	Vona Vona	—	Wind speed	0.33	0.50	<0.01	21
			Zooplankton biomass	0.11			
			Tide range	0.06			
	Tulagi		Days since 25 mm rain	0.31	0.59	<0.005	19
			Temperature	0.25			
			Zooplankton biomass	0.03			
	Overall		Days since 25 mm rain	0.12	0.14	<0.01	62
		—	Days since rain	0.02			
Encrasicholina heterolobus	Munda	—	Total rainfall	0.19	0.30	<0.05	22
		—	Days since rain	0.11			
	Vona Vona	—	Cloud cover	0.32	0.44	<0.01	21
			Moon phase	0.12			
	Tulagi	—	Tide range	0.24	0.24	<0.05	16
	Overall	—	Total rainfall	0.11	0.14	<0.05	59
			Temperature	0.03			
Spratelloides delicatulus	Munda		Moon phase	0.28	0.28	<0.01	22
	Vona Vona		Moon phase	0.26	0.50	<0.01	22
		—	Tide range	0.13			
			Cloud cover	0.11			
	Tulagi		Moon phase	0.51	0.60	<0.005	17
			Cloud cover	0.09			
	Overall	—	Tide range	0.05	0.13	<0.05	61
		—	Zooplankton biomass	0.04			
			Cloud cover	0.04			
Spratelloides lewisi	Munda		Zooplankton biomass	0.22	0.41	<0.05	18
			Days since rain	0.10			
			Cloud cover	0.09			
	Vona Vona		Cloud cover	0.29	0.62	<0.01	15
		—	Wind speed	0.19			
		—	Moon phase	0.14			
	Tulagi	—	Temperature	0.39	0.66	<0.01	14
		—	Zooplankton biomass	0.16			
		—	Days since rain	0.11			
	Overall		Temperature	0.13	0.20	<0.01	47
			Zooplankton biomass	0.07			
Spratelloides gracilis	Vona Vona		Moon phase	0.62	0.82	<0.05	8
			Temperature	0.10			
			Zooplankton biomass	0.10			
Archamia zosterophora	Munda	—	Days since 25 mm rain	0.49	0.65	<0.01	11
		—	Days since rain	0.16			
	Vona Vona		Zooplankton biomass	0.42	0.42	<0.05	10
	Overall	—	Days since 25 mm rain	0.30	0.41	<0.05	21
			Zooplankton biomass	0.11			

negative tide range, cloud cover, and negative zooplankton biomass. When the number of variables were reduced (Table 5), wind and days of rain at Vona Vona and temperature at Tulagi were also significant ($P<0.05$). Among samples from months where spawning had been detected, moon phase and days of rain showed the best fit.

There was significant positive correlation between spawning of *S. lewisi* and zooplankton biomass and days since rain at Munda (Table 4). Lower temperature,

Table 5

Stepwise linear regression models of best fit for six independent proximate stimuli. y = percent spawning; t = temperature; d = zooplankton density; m = moon phase; ti = tidal range; w = wind speed; r = days of rain between samples; r^2 = multiple regression coefficient; P = significance level; N = sample size. Overall includes all samples; spawning includes only months when spawning was detected.

Species	Site	Model	r^2	P	N
Encrasicholina devisi	Munda	y = 0.58 − 0.02r	0.14	<0.08	22
	Vona Vona	y = 3480m + 0.29ti − 0.15w − 3479	0.40	<0.05	21
	Tulagi	y = 0.14t − 0.0003d − 0.18r − 2.89	0.33	<0.07	19
	Spawning	y = 0.52 − 0.006r	0.02	<0.44	40
	Overall	y = 0.50 − 0.0001d − 0.01r	0.07	<0.10	62
Encrasicholina heterolobus	Munda	y = 0.92 − 0.15r	0.08	<0.22	22
	Vona Vona	y = 3741m + 0.0001d − 0.26w − 0.08r − 3742	0.50	<0.05	21
	Tulagi	y = 0.79 − 0.92ti	0.24	<0.05	16
	Spawning	y = 0.10t − 0.57ti − 0.02r − 1.73	0.27	<0.05	33
	Overall	y = 2459m − 0.42ti − 0.02w − 0.01r − 2458	0.16	<0.05	59
Spratelloides delicatulus	Munda	y = 7084m − 0.0001d − 0.37ti − 7083	0.38	<0.05	22
	Vona Vona	y = 10759m + 0.27w + 0.13r − 10759	0.49	<0.01	22
	Tulagi	y = 8825 + 0.11t − 8828m	0.51	<0.005	17
	Spawning	y = 3510m + 0.02r − 3510	0.16	<0.05	38
	Overall	y = 0.57 − 0.36ti	0.05	<0.11	61
Spratelloides lewisi	Munda	y = 0.0003d + 0.17r − 0.39	0.24	<0.13	18
	Vona Vona	y = 5217 − 5216m	0.15	<0.15	15
	Tulagi	y = 1.40 − 0.04t − 0.25ti	0.26	<0.17	14
	Spawning	y = 0.02r − 0.0001d + 0.34	0.30	<0.01	29
	Overall	y = 0.08t − 0.03w + 0.01r − 2.34	0.23	<0.01	47
Spratelloides gracilis	Vona Vona	y = 12588m + 0.56ti − 12587	0.86	<0.05	8
Archamia zosterophora	Munda	y = 4262 − 4262m − 0.49ti	0.50	<0.06	11
	Vona Vona	y = 0.08t − 1.98ti − 0.80	0.94	<0.001	10
	Spawning	y = 3957 − 3956m	0.30	<0.16	8
	Overall	y = 0.72 − 0.79ti	0.46	<0.001	21

low zooplankton biomass, and recent rain explained 66% of the variation in spawning periodicity at Tulagi ($P<0.01$). Cloudy conditions, light winds, and waning moon phases were the variables most correlated with spawning in *S. lewisi* at Vona Vona (Table 4). However, the combined data showed that temperature and zooplankton biomass were the most significant stimuli. These conflicting results were reflected in the second analysis, where the stimuli chosen could not explain a significant amount of the variation in spawning at any site (Table 5).

Correlations between environmental stimuli and the spawning periodicity of *S. gracilis* could only be analysed for fish from Vona Vona. Most variation could be explained by moon phase, temperature, tide, and zooplankton biomass (Tables 4, 5). Most fish spawned at full moon and when temperature, tidal range, and prey biomass were high.

Archamia zosterophora This species was most frequently caught at Munda and Vona Vona where it spawned most often during periods of high rainfall (at Munda), and when zooplankton biomass was high (at Vona Vona) (Table 4). These variables were also the most significant when all data were combined. When these variables were excluded from the analysis (Table 5), lower tidal range and higher temperatures (Vona Vona) were the only significant stimuli.

Discussion

Size-at-sexual-maturity of some *Encrasicholina* and *Spratelloides* species from the Solomon Islands varied both locally and compared with other studies elsewhere in the South Pacific.

Encrasicholina heterolobus and *S. gracilis* reached sexual maturity at smaller lengths than previously reported (Tham 1965; Tiews et al. 1971; Dalzell and Wankowski 1980; Conand 1985; Dalzell 1985, 1987b). Such differences may be partly an artifact of the different sexual maturity criteria used. The present study,

unlike others, used histological examination of gonads to verify macroscopic stages.

In the Solomon Islands, *Encrasicholina devisi* reached sexual maturity at 45 mm, and some fish at this size were in spawning condition. This is consistent with results from Papua New Guinea (Dalzell and Wankowski 1980), New Caledonia (Conand 1985), and southern India (Luther 1979). *Spratelloides delicatulus* also showed little difference throughout the region in length-at-sexual-maturity (Lewis et al. 1983, Conand 1985, McCarthy 1985).

Spratelloides lewisi showed local variation in length-at-sexual-maturity. Fish from Tulagi were not sexually mature at less than 40 mm (compared with 35 mm at other sites) and they also grew to a greater size than fish from the other sites (unpubl. data).

Length-at-first-spawning, however, was similar for both *Encrasicholina* species and *S. delicatulus* throughout the region (Dalzell and Wankowski 1980, Lewis et al. 1983, Conand 1985), except for *E. heterolobus* at Munda, where fish were in spawning condition at a smaller length than at the other sites in the Solomon Islands.

Both *Spratelloides lewisi* and *S. gracilis* showed variation in length-at-first-spawning between sites. At Tulagi, *S. lewisi* did not spawn until a much greater length was attained. These results are consistent with those of Dalzell (1987), who found a difference of 9 mm in the length-at-first-spawning in two populations of *S. lewisi* in Papua New Guinea waters. Dalzell (1985) also found that Papua New Guinea *S. gracilis* did not develop ripe eggs until 44 mm, which was much larger than the length-at-first-spawning of fish from the Solomon Islands (35 mm). Unfavorable conditions for reproduction may delay the onset of gonadal development in these species at some sites to help offset reproductive uncertainty (Mann and Mills 1979).

No comparative data on length-at-sexual-maturity of *A. zosterophora* are available, and there are few data for other similar-sized apogonids. However, this species matures at almost 80% of maximum size, which is larger than in the clupeoids (70%). The subtropical Australian species *Apogon fasciatus* also matures at about 70% of maximum size (90 mm) near Brisbane (K. Warburton, Zool. Dep., Univ. Queensland, Brisbane, Australia, unpubl. data).

The relationship between length-at-first-spawning and maximum length of the Solomon Islands baitfish closely fits that found for other clupeoids (Beverton 1963). Beverton (1963) showed that length-at-first-spawning among clupeoids is closely proportional to maximum length, with smaller species spawning at a smaller size (relative to their maximum) than larger ones (Blaxter and Hunter 1982). Longhurst and Pauly (1987) hypothesize that length-at-sexual-maturity and maximum length are determined by the interactions of oxygen supply and demand. Any species of fish living in cold water should grow to a greater size and mature at a larger size than the same species in warm water, given similar food supplies. Water temperature at Tulagi was consistently 1–2°C colder than at the other sites, and this may account for differences in these parameters in *S. lewisi* at this site. The regional differences seen in *E. heterolobus* and *S. gracilis* also support this idea, with fish from higher latitudes maturing at greater lengths. However, similar patterns were not found in the other species. Availability of food also must play an important role by affecting growth rates.

Many clupeoids, including most engraulids, are multiple spawners (Blaxter and Hunter 1982), and studies of other engraulids suggest they spawn batches of eggs every 2–10 days (Hunter and Goldberg 1980, Alheit et al. 1984, Clarke 1987). Smaller species (e.g., *Encrasicholina purpureus*) spawn more frequently during the peak spawning period (as often as every 2 days; Clarke 1987). The spawning frequency of multiple spawning fish can be determined by the presence or absence of postvitellogenic follicles in the ovaries; their presence indicates that a fish has spawned within the previous 24–48 hours (Hunter and Goldberg 1980). Clarke (1987) reported that postvitellogenic follicles were distinguishable in *Encrasicholina purpureus* up to 16 hours after spawning. In our study, we did not find either postvitellogenic follicles or a continuous egg-size distribution indicative of multiple spawning (Blaxter and Hunter 1982). However, the similarity in reproductive behavior of *Encrasicholina* species and the presence of eggs in the plankton throughout most of the year suggest that *E. devisi* and *E. heterolobus* are also multiple spawners. Our data on *Encrasicholina devisi* and *E. heterolobus* were consistent with that of Leary et al. (1975) on *Encrasicholina purpureus*. We found, as had Leary et al., only two egg sizes: one advanced and one with all eggs at the yolk-precursor stage of development. Leary et al. (1975) interpreted these results to indicate that *E. purpureus* spawned once in its lifetime. However, Clarke (1987) found that *E. purpureus* eggs could mature very rapidly, and hence timing of sampling was critical. Running-ripe eggs were only present shortly before spawning, which occurred one or two hours after sunset. If *E. devisi* and *E. heterolobus* are batch spawners similar to *E. purpureus*, then we would expect to collect only fish about to spawn in our samples, as the postvitellogenic follicles of fish that spawned the previous night would have degraded (Clarke 1987). However, spawning is probably less frequent than in the smaller *E. purpureus* because greater energy is required by larger fish to maintain continuous spawning (Hunter and Leong 1981).

Ovaries of the three species of *Spratelloides* and *A. zosterophora* all contained only a single size-group of developing oocytes, which suggests that they spawn all the eggs in the ovaries at once. Whether a female develops another batch of eggs after spawning was not determined. However, given the high proportion of female *Spratelloides* spawning at any time, it seems probable that each female produces more than one batch of eggs. Most apogonids are mouth-brooders (Thresher 1984), and other species have been found with eggs in their buccal cavity that are at more than one stage of development, which suggests that they are multiple spawners (Thresher 1982).

Flexibility in reproduction is well documented among a range of animals and usually involves a direct physiological response to nutrient level or some associated environmental cue (Giesel 1976). Extended breeding seasons are a common phenomenon among tropical fishes, particularly coral reef fish (Munro et al. 1973, Russell et al. 1977, Johannes 1978, Lowe-McConnell 1979, Walsh 1987). The present work, and other studies of *Encrasicholina*, *Spratelloides*, and apogonid reproduction (Leary et al. 1975; Russell et al. 1977; Dalzell and Wankowski 1980; Dalzell 1985, 1987ab; Conand 1985; McCarthy 1985; Clarke 1987), found that the spawning season of these fish is protracted, with some individuals in the population spawning at any time during the year. There are also periods when most of the population is spawning. If reproduction were controlled only by endogenous cycles and females spawned as soon as they were physiologically capable, then as the proportion of larger fish increased there should be a greater proportion of spawning fish in the population. Examination of our data failed to find any significant relationship between the proportion of larger fish and the proportion spawning for any species at any site. Non-parametric tests also showed that the frequency of major spawnings was not random. Hence it is unlikely that spawning periodicities shown by baitfish are a result of intrinsic mechanisms. The timing and intensity of periods of increased spawning activity appear to be highly variable, linked to exogenous stimuli and with no endogenous rhythms.

Of the several hypotheses put forward to explain the timing of fish reproduction, one of the more widely accepted is the "match-mismatch" hypothesis of Cushing (1967). This proposes that if the timing of reproduction coincides with peaks in the plankton cycle, larval survival is enhanced. Timing of peak plankton production does not necessarily occur at exactly the same time each year, so if fish are serial spawners they can exploit the plankton cycle well (e.g., California sardine) by spawning during any of the months of spring or summer when food becomes superabundant (Cushing 1975). Much of the data to support this hypothesis comes from temperate waters, but data on the reproduction of tropical clupeoids from open oceans also support this hypothesis (Longhurst 1971, Roy et al. 1989).

Johannes (1978) proposed that coastal tropical fish tend to spawn at times and locations that will reduce predation on larvae by transporting them out of the adult habitat, while enabling them to return to suitable areas for postlarval settlement. At many sites, periods of major spawning coincide with low winds and full moon. The baitfish species studied here spawn in lagoons fringed by coral reefs, where water currents are negligible. Both adults and larvae are pelagic and live in the deeper waters of the lagoon. When the larvae are abundant, adults prey on them (Milton et al. 1990). If deeper waters of the lagoon are the favored habitat, then according to Johannes' hypothesis (1978) adults should spawn when local flushing is greatest (spring tides) but regional flushing is least (low winds) to ensure larvae develop in the same area.

Although baitfish spawn throughout the year, with no consistent seasonal pattern, there appears to be some regularity in their spawning. At each site, certain proximate factors were significant for more than one species. This suggests that if these fish are responding to exogenous spawning stimuli, their influence must be interposed by local hydrography and topography. At Vona Vona, spawning by five of the six species examined was correlated with moon phase. Both *Encrasicholina* and two *Spratelloides* species spawned around the full moon, while *S. lewisi* spawned around the new moon. Both *Encrasicholina* species also spawned when wind strength was reduced. The spawning around phases of the moon has often been assumed to be related to increased tidal exchange during spring tides (e.g., Johannes 1978, Walsh 1987). However, in this study greater tidal range at any site was not directly correlated with moon phase (Table 3). Vona Vona is an enclosed lagoon with many islands and patch reefs. In this habitat, spawning around the full or new moon does not appear to be related to the potential to flush eggs and larvae to more favorable habitats by tidal water movement (Johannes 1978). Possibly, spawning around the full moon when the wind is reduced may increase spawning success by increasing visibility at night (during spawning) and reducing the dispersal of eggs, and hence increasing the chances of fertilization. This hypothesis would also explain the strong negative relationship between spawning by *A. zosterophora* and tidal range at this site.

Moon phase was the single variable most often correlated with spawning in this study, both for five species at one site (Vona Vona) and for one species at different sites (*S. delicatulus*). However, our data do not indicate a strong relationship with moon phase for either *Encrasicholina* species at Munda or Tulagi. This

suggests that either local conditions exert a strong influence on the timing of reproduction in these species or that at these sites reproduction is not strongly linked to particular environmental events. Wright (1989) also found no relationship between spawning by *E. heterolobus* in Indonesia and temperature, rainfall, or tidal phase, and suggested that these factors were not influencing spawning.

However, among the other species, temperature and reduced tidal range appear to be more important at Tulagi. Higher temperatures should allow increased growth under favorable conditions, and reduced tidal exchange would reduce egg movement away from favorable habitats.

While rainfall has been suggested as a proximate factor influencing spawning by *Encrasicholina* species in Papua New Guinea (Dalzell and Wankowski 1980; Dalzell 1984, 1987b), in our study rainfall was only weakly correlated with spawning of *Encrasicholina* at Munda (Tables 4, 5). Spawning appeared to be greater during periods of lower rainfall. Positive relationships between spawning and time since rain or less rain may be indirectly linked to phytoplankton production, which is determined by light or the depth of mixing (Wyatt 1980). Variations in wind strength and cloudiness will cause major variations in the onset and end of the phytoplankton production cycle (Blaxter and Hunter 1982). If rainfall at Munda is linked to the phytoplankton cycle, spawning during periods of low rainfall would be consistent with Cushing's (1967) hypothesis. Some previous studies in southeast Asia and Papua New Guinea (Tiews et al. 1971, Sitthichockpan 1972, Dalzell 1987b) have suggested that *Encrasicholina* spawned more intensively during the months of peak zooplankton production.

The variation in spawning frequency observed among the species in this study suggests that each responds differently to local conditions, reacting to those variables most appropriate to maximize reproductive success in the immediate environment (Bye 1984). No obvious differences were detected in baitfish spawning patterns between the exploited fishing grounds and the unexploited site. If baitfish numbers are higher at the unexploited site, this suggests, in turn, that differences in the observed spawning patterns were not density-dependent. Lack of clear proximate stimuli for spawning among the six species examined makes it difficult to predict the timing of major spawning events by these species.

However, protracted spawning and the baitfish population's adaptation to local conditions suggests that these species should be resilient to increased fishing mortality. Factors affecting larval survival and growth may be more important in determining recruitment to the fishery.

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Abstract.—A biochemical examination of otolith growth–somatic growth relationship was conducted in rainbow trout *Oncorhynchus mykiss*. The rate of otolith growth was defined by calcium deposition on otoliths in an *in vitro* isolated preparation of otolith-containing sacculi. Somatic growth was estimated by RNA-DNA ratios in white trunk muscle. Rainbow trout weighing approximately 120 g were starved for 5 days and then fed commercial trout pellets once a day. They were sampled on days 1, 2, 3, and 5 after starvation, and on days 1, 2, 3, and 4 after feeding. In a separate experiment, fish were sampled at 6-hour intervals of 1000, 1600, 2200, and 0400 hours over a 24-hour period. Otolith and somatic growth showed a positive relationship, both decreasing from 2 days after starvation and recovering on day 4 after feeding. In otoliths, however, the starvation-induced decrease in calcium deposition was transiently restored on day 1 after feeding, followed by a decrease on day 2. The diel relationship between otolith and somatic growth was coupled, showing minimum levels at 2200 hours. These results suggest that otolith growth ordinarily reflects somatic growth rates on the daily basis.

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Biochemical Relationship Between Otolith and Somatic Growth in the Rainbow Trout *Oncorhynchus mykiss*: Consequence of Starvation, Resumed Feeding, and Diel Variations

Yasuo Mugiya
Hirotaka Oka

Faculty of Fisheries, Hokkaido University
Minato-3, Hakodate 041, Japan

Teleost otoliths are calcium carbonate concretions which have increments consisting of a bipartite structure of light and dark rings. These structures are known to be formed on a daily basis (Pannella 1971). Since otolith and fish size are highly correlated for a variety of marine and freshwater species (Campana and Neilson 1985), it is possible to estimate growth-rate histories of individual fish by measuring the width of otolith increments. Volk et al. (1984) averaged otolith increment widths over each week and found a linear regression of mean increment width with somatic growth rate in chum salmon *Oncorhynchus keta* under controlled feeding. Nishimura and Yamada (1988) successfully back-calculated the growth rate of walleye pollock *Theragra chalcogramma* by using mean otolith width measured every 10 increments. However, it remains to be shown whether the rate of otolith growth reflects somatic growth rates in terms of daily or subdaily trends.

Recently several workers (Secor and Dean 1989, Reznick et al. 1989, Wright et al. 1990) reported an uncoupling of the relationship between otolith and somatic growth in fish populations experiencing slow and fast somatic growth. Similar uncoupling was exaggeratedly induced in hypophysectomized goldfish *Carassius auratus*, in which somatic growth in length was completely inhibited but otolith continued to grow at a reduced rate (Mugiya 1990).

Since the otolith (sagitta) occurs within the sacculus which is anatomically closed in rainbow trout *Oncorhynchus mykiss*, it is feasible to take out the otolith-containing sacculus without any leakage of the endolymph (Mugiya 1984). An *in vitro* preparation of the isolated sacculi was used for indicating the current growth rate of otoliths, which reflected the *in vivo* physiological state at the time when the fish were sampled (Mugiya 1984, 1987). Somatic growth is a balance between catabolic and anabolic components in protein metabolism (Miglavs and Jobling 1989). Since accretive growth should be directly associated with protein synthetic capacity, RNA-DNA ratios in muscle are widely used as an indicator of the short-term or current somatic growth rate (Bulow 1987).

The aim of the present study is to clarify the biochemical relationship between otolith and somatic growth on a daily basis, using starved and then fed rainbow trout. The otolith growth–fish growth relationship was also examined at 6-hour intervals

over a 24-hour period. Otolith and somatic growth were defined by the rate of *in vitro* calcium deposition on otoliths and RNA-DNA ratios in white trunk muscle, respectively. Serum calcium concentrations were examined for diel variations based on previous work on the relationship between serum calcium and otolith growth (Mugiya 1984).

Materials and methods

We performed two experiments with food and diel effects on somatic and otolith growth. Immature rainbow trout *Oncorhynchus mykiss* weighing 100–130 g were obtained from a trout farm and acclimated to experimental conditions for at least 4 weeks before use. Throughout the acclimation and experimental periods, they were maintained in a pair of outside concrete ponds ($3.8\,m^2 \times 0.7\,m$ in depth) which were supplied with running water at $14 \pm 0.5°C$, and fed commercial trout pellets once a day at around 1500 hours, unless otherwise stated. The ration fed was about 1.5% of body weight.

Starvation and refeeding

This experiment was carried out in October 1988. Dusk occurred at 1700 hours and dawn at 0545 hours. Sixty fish were randomly divided into two groups (30 fish per group), and separately assigned to one compartment of the paired ponds. One group was starved for 5 days and then fed. During these periods, they were sampled on days 1 (43 hours from last feeding), 2, 3, and 5 after starvation, and on days 1 (19 hours from the first refeeding), 2, 3, and 4 after refeeding. The other group was fed throughout the period and sampled as the control on the same time schedule, except on the third day of starvation and on the second day of refeeding when only the experimental group was sampled. Sampling was conducted alternately between experimental and control groups at 0945–1045 hours every day. At each sampling, 4–6 fish were gently netted one at a time, and immediately bled by cutting the tail of the fish. After bleeding, a pair of sacculi containing otoliths were isolated, placed in an incubation medium, and then the next fish was netted. The remaining part of the body was stored at −40°C and analyzed within 5 days for RNA-DNA ratios. Data from the control group were pooled for statistical analyses, as little difference was found among the sampling days.

Diel variation

This experiment was carried out in December 1988. Dusk occurred in 1600 hours and dawn at 0700 hours. To examine the diel relationship between otolith and somatic growth, 25 fish were stocked in each compartment of the paired ponds, and 7 fish each were randomly sampled at 6-hour intervals of 1000, 1600, 2200, and 0400 hours over a 24-hour period. Sampling was conducted alternately from one compartment at 1000 and 2200 hours, and from the other compartment at 1600 and 0400 hours. This sampling regime is recommended for minimizing handling effects. After fish were netted one at a time, blood was immediately collected from the caudal vessels by cutting the tail of the fish and draining it into test tubes. After centrifugation, the separated sera were stored at −40°C for 6–24 hours and analyzed for total calcium concentrations by flame photometry using an atomic absorption spectrophotometer (Hitachi #518). After the blood collection, sacculi were isolated for incubation, and the remaining part of the body was stored for RNA and DNA analyses. In this experiment, the fish were starved throughout the sampling day.

Otolith incubation

Otolith-containing sacculi were isolated according to a previously described technique (Mugiya 1987). Isolated sacculi were incubated in 50 mL of a Ringer solution (Mugiya 1986) containing ^{45}CA (New England Nuclear) at a concentration of 1×10^4 Bq/mL. Incubation was carried out with oxygenation at 14°C for 2 hours.

After incubation, sacculi were rinsed several times in ^{45}CA-free Ringer solution and the otoliths were separated under a binocular microscope. The separated otoliths were lightly rinsed in water, placed in each counting vial, dried overnight at 80°C, and then weighed. They were solubilized in a mixture of 0.2 mL perchloric acid and 0.2 mL hydrogen peroxide (Mugiya 1987), and added to Scintisol EX-H (Wako Chem.) for radioactive counting (liquid scintillation spectrometer, Aloka LSC-673). The rate of otolith growth was evaluated in terms of micrograms of calcium deposited per unit otolith weight.

RNA and DNA determinations

RNA-DNA ratios were estimated in the white muscle collected from an area of the dorsoanterior trunk, using a modification of the Schmidt and Thannhauser method (Buckley and Bulow 1987). Briefly, white muscle (1.00 g) was homogenized with cold distilled water and adjusted to 10.0 mL. A 1.4-mL aliquot of the homogenate was used for the estimation of nucleic acids. RNA and DNA were purified with 0.6 N cold $HClO_4$, and then extracted with 0.3 N KOH and 0.6 N hot $HClO_4$, respectively. Both acids were quantified from the absorbance of the extracts at 260 nm. RNA and DNA

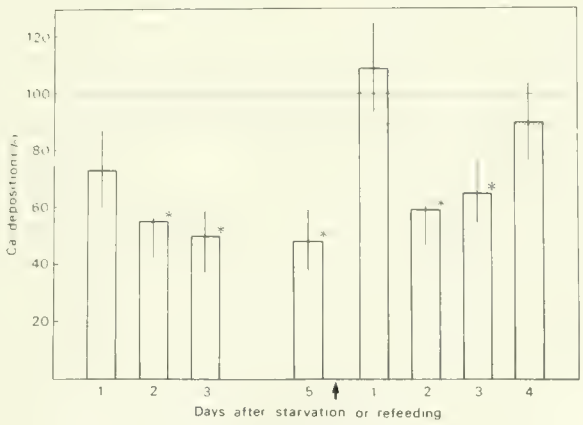

Figure 1

Percentage effects of starvation and refeeding on *in vitro* calcium deposition on otoliths in *Oncorhynchus mykiss*. Control values are pooled and the mean level (horizontal bar) is shown with SE of 48 otoliths. Vertical bars represent mean ± SE of 3–10 otoliths. Arrow indicates time when fish were refed. $^{*}P<0.05$.

Table 1

Effects of starvation and refeeding on muscle RNA and DNA concentrations (mg/g) in rainbow trout *Oncorhynchus mykiss*.

	RNA	DNA
Control	1.51 ± 0.03	0.61 ± 0.02
Starvation (days)		
1	1.50 ± 0.06	0.56 ± 0.02
2	1.21 ± 0.08*	0.58 ± 0.01
3	0.90 ± 0.04**	0.65 ± 0.02
5	0.89 ± 0.04**	0.68 ± 0.04
Refeeding (days)		
1	0.88 ± 0.07**	0.65 ± 0.06
2	0.97 ± 0.06**	0.61 ± 0.02
3	1.07 ± 0.02**	0.66 ± 0.01
4	1.57 ± 0.04	0.63 ± 0.02

Values are mean ± SE of 26 and 4–6 fish for control and experimental groups, respectively.
$^{*}P<0.05$; $^{**}P<0.01$.

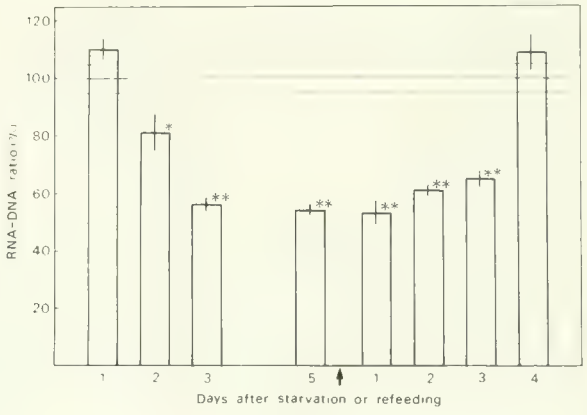

Figure 2

Percentage effects of starvation and refeeding on RNA-DNA ratios in white trunk muscle in *Oncorhynchus mykiss*. Control values are pooled and the mean level (horizontal bar) is shown with SE of 26 fish. Vertical bars represent mean ± SE of 4 or 6 fish. Arrow indicates time when fish were refed. $^{*}P<0.05$; $^{**}P<0.01$.

standard solutions were prepared using RNA from yeast and DNA from salmon sperm (Wako Chem.).

Statistics

Student's t-test for unpaired observations was applied to assess statistical significance of differences between mean values. Significance was accepted at $P<0.05$.

Results

Starvation and refeeding

The rate of *in vitro* calcium deposition on otoliths ranged from 0.06 to 0.08 μg/mg · hour in the control group. These data are pooled and presented as the mean level with standard errors (Fig. 1). Effects of starvation and refeeding on the rate are expressed as a percentage against the control level. Starvation induced an inhibitory effect ($P<0.05$) on the rate of calcium deposition on otoliths by day 2, decreasing to approximately half of the control. This level remained almost unchanged until day 5, the last day of starvation. On refeeding, the starvation-induced decrease recovered to the control level as early as day 1. However, this recovery was transient, followed by a significantly ($P<0.05$) reduced calcium deposition on day 2. This reduced calcium deposition recovered to the control level on day 4 after refeeding (Fig. 1).

Muscle RNA and DNA concentrations and their ratios are presented in Table 1 and Figure 2, respectively. Starvation and refeeding affected RNA concentrations, but DNA concentrations remained constant during the experiment (Table 1). Therefore, changes in RNA-DNA ratios are primarily attributable to changes in RNA concentrations.

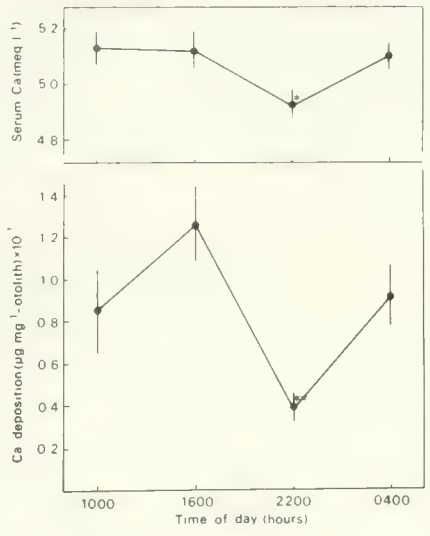

Figure 3

Diel variations in serum calcium concentrations (upper graph) and *in vitro* calcium deposition on otoliths (lower graph) in *Oncorhynchus mykiss*. Each plotted value represents mean ± SE of 7 fish for serum calcium and of 12–14 otoliths. $^{*}P<0.05$ for 1600 hours; $^{**}P<0.001$ for 1600 hours.

Table 2

Diel variations in muscle RNA and DNA concentrations (mg/g) in rainbow trout *Oncorhynchus mykiss*.

Time of day (h)	RNA	DNA
1000	1.26 ± 0.08	0.66 ± 0.04
1600	1.30 ± 0.08	0.72 ± 0.02
2200	0.66 ± 0.04*	0.76 ± 0.06
0400	0.80 ± 0.04	0.68 ± 0.04

Values are mean ± SE of 7 fish.
$^{*}P<0.01$ for 1600 hours.

RNA-DNA ratios ranged from 1.91 to 2.73, with a mean value of 2.44 in the control group. One day's starvation had no effect on the ratio (Fig. 2). The first significant ($P<0.05$) effect occurred on day 2 after starvation, followed by further decrease to approximately half of the control on day 3. This reduced level apparently remained essentially unchanged through day 5. In contrast to the response observed for otoliths, refeeding had no effect on the recovery in RNA-DNA ratios the next day (Fig. 2). Ratios increased gradually with feeding and recovered to the control level on day 4 after refeeding.

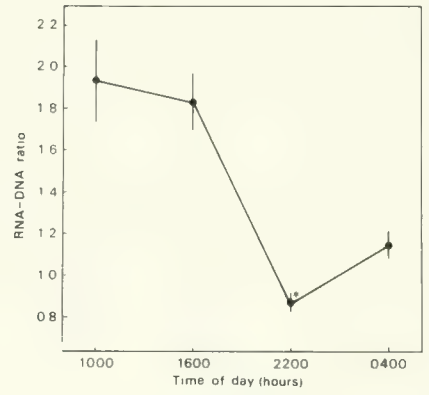

Figure 4

Diel variations in RNA-DNA ratios in white trunk muscle in *Oncorhynchus mykiss*. Each plotted value represents mean ± SE of 7 fish. $^{*}P<0.001$ for 1600 hours.

Diel variation

Serum calcium concentrations varied dielly by approximately 4%, and this variation was statistically significant at $P = 0.05$ (Fig. 3). Calcium concentrations were high during the daytime, but a nadir occurred at 2200 hours.

The profile of diel variations in calcium deposition on otoliths was essentially the same as that of serum calcium concentrations (Fig. 3). The high rate of calcium deposition at 1600 hours rapidly decreased by 70% ($P<0.001$) to a nadir at 2200 hours, followed by an increase toward 0400 hours.

Diel variations in muscle RNA and DNA concentrations and their ratios are presented in Table 2 and Figure 4, respectively. Diel variations were significant in RNA concentrations and RNA-DNA ratios. The profile of variations in the ratios was similar to that of calcium deposition on otoliths: high ratios during the daytime were followed by a steep decrease between 1600 and 2200 hours. The lowest ratio occurred at 2200 hours, and this ratio was highly significant ($P<0.001$) compared with the ratio at 1600 hours. Differences between 1000 and 1600 hours were not statistically significant in either otolith or muscle, showing that the criterion of similar growth profiles was fulfilled.

A comparison of variations in calcium deposition on otoliths and RNA-DNA ratios in muscle showed positive relationships through several days after starvation and during the diel experiment. However, uncoupling was found in the recovery processes with refeeding: calcium deposition on otoliths transiently recovered on day 1 after refeeding, while RNA-DNA ratios did not (compare Figures 1 and 2).

Discussion

RNA-DNA ratios in muscle have been widely accepted as an index of current somatic growth rates in various species of marine and freshwater fish (Bulow 1987). These ratios are affected by various factors such as season (Bulow et al. 1981), ration size (Bulow 1970, Buckley 1979, Wilder and Stanley 1983, Jürss et al. 1986), temperature, salinity (Jürss et al. 1987), and lunar cycles (Farbridge and Leatherland 1987). Various toxicants also reduce the ratios (Barron and Adelman 1984). The present study presents an additional finding with regard to variations of RNA-DNA ratios: the ratios had distinct diel variations, showing higher values during daytime than nighttime. It is desirable to confirm such a profile of variations by further examinations at shorter and longer time-intervals.

Endocrinologically, RNA-DNA ratios are under the control of growth-regulating hormones. Hypophysectomy reduced the ratios, and replacement therapy with beef growth hormone restored the ratios to a normal level in bullheads *Ictalurus melas* (Kayes 1979). Circadian periodicities in the surge of growth-regulating hormones are well documented in higher vertebrates (Kato et al. 1982). Although few comparable references are available in fish, cyclic variations in growth hormone have been reported in plasma and pituitary levels in salmonids (Leatherland et al. 1974, Leatherland and Nuti 1982, Bates et al. 1989). Therefore, the cyclic surge of this hormone in combination with other hormones is probably a cause for diel variations in RNA-DNA ratios in the present fish.

Effects of starvation or restricted food on RNA-DNA ratios have been repeatedly reported. A 4-week starvation induced an approximately 40% decrease in the ratios in rainbow trout *Oncorhynchus mykiss* (Jürss et al. 1986). Brook trout *Salvelinus fontinalis* also had the ratio reduced by 44% after 22 days of restricted feeding (Wilder and Stanley 1983). Bulow (1970) showed that RNA-DNA ratios directly reflected different somatic growth rates induced by nutritional manipulation. However, it is not clear how fast food deprivation affects this ratio. Although the time course of the effect will depend on various factors such as temperature, fish sizes, sexual status, etc., the present study revealed that the first effect of starvation on RNA-DNA ratios in muscle appeared on day 2 (67 hours from last feeding) in adult rainbow trout *Oncorhynchus mykiss*. This inhibitory effect was exaggerated with time, but the ratios never decreased below half the control level even on day 15 after starvation (data are not presented here). This level (55% of the control) is similar to trout values in the literature mentioned above, and therefore it appears to be a basal level in RNA-DNA ratios in white muscle of rainbow trout.

Starvation-induced decrease in RNA-DNA ratios recovered with the resumption of daily feeding at a level of 1.5% of body weight. The recovery processes were rather steady, taking 4 days in the present study. Bulow (1970) showed a more rapid recovery in golden shiners *Notemigonus crysoleucas*: 2 days feeding at 6% body weight seemed to be enough for the recovery of a starvation-induced decrease in ratios to the normal level. This disparity may be explained by the amount of food used and/or species difference. Lied et al. (1983) reported that a starvation-induced decrease in RNA-DNA ratios recovered to the normal level within 8 hours after refeeding *ad libitum* in cod *Gadus morhua*. However, it is uncertain whether this recovery was due to the result of food assimilation or to diel variations in the ratios, because control values were not available at each determination time in the study.

Recently Miglavs and Jobling (1989) reported that a growth spurt (compensatory growth) transiently occurred following realimentation after a period of food restriction in juvenile Arctic char *Salvelinus alpinus*. Nevertheless, no corresponding increase occurred in tissue RNA-DNA ratios. This led them to present a limit to using the ratios as a growth index. However, since their somatic growth rate was calculated from a cumulated increase in body weight for 28 days, it is uncertain whether or not the rate remained high on the last day, when the RNA-DNA ratios were determined.

When somatic and otolith growth rates were biochemically compared at 6-hour intervals over a 24-hour period, or after food deprivation, they were coupled at a qualitative level. In spite of these positive relationships, evidence of an allometric relationship between otolith and somatic growth has been accumulated, especially under suboptimal conditions. For example, Mosegaard et al. (1988) examined the effect of temperature, fish size, and somatic growth rate on otolith growth rate in Arctic char *Salvelinus alpinus* and found an uncoupling between somatic and otolith growth rates at hyperoptimal temperatures. Based on these results, they suggested that metabolic activity, not necessarily somatic growth rate, governs otolith growth rate. Somatic growth rate results mainly from the balance between protein synthesis and degradation, and hyperoptimal temperatures would accelerate both components, especially degradation, resulting in no somatic growth (Houlihan et al. 1988). However, since somatic growth is comparable with components from metabolic rates within the range of optimal temperatures (Webb 1978), the muscle RNA-DNA ratio, an index for protein synthesis, will be a reflection of metabolic components at an appropriate temperature. Therefore, it appears reasonable to use this ratio for examining the relationship between somatic and otolith growth rates, even if otolith growth is a function of metabolic rate.

In the present study, the transient recovery of otolith growth occurred on the first day following refeeding. Although the definite reason for this remains unexplained, an accelerated recovery process after growth suppression is well known as "repletion" in mammalian skeletal tissue formation (Linkhart et al. 1988). Mechanisms for repletion would differ depending on tissues. Since the otolith is an acellular product secreted by otolith-forming cells (Saitoh and Yamada 1989), a possible explanation for otolith repletion is as follows: Starvation may interrupt the releasing activity partly due to the reduced processing of the secretory product. This would inversely result in some accumulation of otolith precursor materials in the cells (Anderson and Capen 1976). Refeeding stimulates release of the accumulated precursors through some factors (e.g., calcium-calmodulin interaction; Mugiya 1986) regulating the secretory activity. A steady-state recovery in synthesis and processing of the secretory product is probably a time-consuming process, running parallel to the recovery of RNA-DNA ratios in muscle. These possibilities await further examination.

In the present study, we have demonstrated corresponding variations in otolith calcification and RNA-DNA ratios in muscle, but a causal relationship between specific growth rate and otolith calcification remains to be studied.

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Western Atlantic Tonguefishes of the *Symphurus plagusia* Complex (Cynoglossidae: Pleuronectiformes), with Descriptions of Two New Species*

Thomas A. Munroe

Systematics Laboratory, National Marine Fisheries Service, NOAA
National Museum of Natural History, Washington, DC 20560

Abstract. – Western Atlantic tonguefishes of the *Symphurus plagusia* (Schneider, in Bloch and Schneider 1801) complex are distinguished from other Atlantic *Symphurus* species by the possession of 12 caudal fin rays, a 1-4-3 pattern of interdigitation of dorsal-fin pterygiophores and neural spines, absence of a pupillary operculum, reduced or absent dentition on ocular-side jaws, and an unpigmented peritoneum. Considerable taxonomic uncertainty has been associated with nominal species of this complex, but the most common practice has been to recognize one widespread species (*S. plagusia*) with two subspecies ranging from the Caribbean southward to Uruguay, and a second species, *S. civitatium* Ginsburg 1951, occurring in inshore areas along the southeastern and Gulf of Mexico coasts of the United States and northern Mexico. The validity of *S. civitatium* is confirmed in this study. Examination of tonguefishes from the Caribbean and southward indicates that specimens previously identified as *S. plagusia* do not comprise one species with two allopatric subspecies, but rather four largely sympatric, albeit not necessarily syntopic, species. *Symphurus plagusia*, the first described species in this complex, occurs in inshore habitats ranging from the Caribbean to Rio de Janeiro. *Symphurus tessellatus* (Quoy and Gaimard 1824), removed from the synonymy of *S. plagusia*, occurs in nearshore, estuarine, and neritic waters throughout the Caribbean southwards to Uruguay. Two new species, *S. oculellus* occurring in neritic waters off northern South America (Guyana to northern Brazil), and *S. caribbeanus* (nearshore habitats throughout the Caribbean), are described and figured. A key to the western Atlantic species of this complex is provided.

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Shallow-water symphurine tonguefishes possessing 12 caudal fin rays, a 1-4-3 pattern of interdigitation of dorsal pterygiophores and neural spines, with reduced or absent dentition on ocular-side jaws, an unpigmented peritoneum, and lacking a pupillary operculum comprise the *Symphurus plagusia* (Schneider, in Bloch and Schneider 1801) complex.** Five western Atlantic and several eastern Pacific species of tonguefishes are recognized in this complex. Throughout the western Atlantic, from North Carolina, U.S.A., to Uruguay (Ginsburg 1951, Menezes and Benvegnú 1976, Munroe 1987), these commonly collected tonguefishes are abundant locally in estuarine and nearshore habitats as well as on sandy or muddy substrates on the inner continental shelf (Meek and Hildebrand 1928, Ginsburg 1951, Lowe-McConnell 1962, Caldwell 1966, Cervigon 1966, Carvalho et al. 1968, Palacio 1974, Menezes and Benvegnú 1976, Lema and Oliveria 1977, Lema et al. 1980, Munroe 1987).

Nomenclatural uncertainty and questions regarding taxonomic validity have been associated with these western Atlantic tonguefishes since the first description of a species from Jamaica by Browne (1756). Much of the confusion centers on species collected in shallow waters of the Caribbean and coastal seas of Central America and much of South America. At least ten combinations of names have been used for these tropical western Atlantic, shallow-water tonguefishes.

Historically (Kaup 1858, Jordan and Evermann 1898, Chabanaud 1949), Atlantic members of this species complex were long regarded as comprising populations of a single widespread, polytypic species, *Symphurus plagusia*. This nomenclatural arrangement began with Kaup (1858) and has continued to the present (Jordan and Goss 1889, Jordan and Evermann 1898, Ginsburg 1951, Menezes and Benvegnú 1976, Rosa 1980, Lucena and Lucena 1982). Ginsburg considered the tropical western Atlantic members of this complex to represent two allopatric subspecies, and his newly-described *S. civitatium* with its disjunct northern distribution, perhaps representing a third subspecies of one wide-ranging polytypic species. However, the most recent review of *Symphurus* of southern South America (Menezes and Benvegnú 1976) questioned recog-

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** There is another western Atlantic tonguefish, *S. plagiusa* (Linnaeus), completely allopatric from *S. plagusia*, which unfortunately has a nearly identical spelling for its specific epithet. It is emphasized that these are completely different and distinctive species that should not be confused because of similarities in their names.

nition of only one species in the tropical western Atlantic region.

My examination of approximately 1000 specimens of *Symphurus* possessing 12 caudal fin rays and a 1-4-3 interdigitation pattern, collected in inshore waters from North Carolina, throughout the Gulf of Mexico and Caribbean, to Uruguay, reveals that previous studies failed to recognize the presence of multiple sympatric species among their material. Neither the hypothesis of multiple populations within a single polytypic species, envisioned especially by Jordan and co-workers, nor Ginsburg's hypothesis of one widespread polytypic species comprised of allopatric subspecies, adequately explain the divergent morphological variation observed in the specimens and the sympatric (sometimes syntopic) occurrences of specimens with different morphological attributes. Instead, the present study recognizes not one, but rather five, western Atlantic members of the *S. plagusia* complex, which are somewhat phenetically similar species that differ in morphology and pigmentation. Four of these species have largely sympatric, but not necessarily syntopic, distributions. The fifth species, *S. civitatium* Ginsburg 1951, is completely allopatric to the others, occurring along the southeastern and Gulf coasts of the United States and northern Mexico.

Three species in this assemblage, *S. plagusia*, *S. tessellatus* (Quoy and Gaimard 1824), and *S. civitatium*, were described previously. Two additional species are described herein. Available taxonomic and ecological information is summarized, differential diagnoses are provided for each species, and a key to identification of the five species is included.

Materials and methods

Methods for counts and measurements and general terminology follow Munroe and Mahadeva (1989) and Munroe (1990). Meristic data, exclusive of scale counts, were taken from radiographs. ID pattern refers to the pattern of interdigitation of dorsal pterygiophores and neural spines. In species accounts, total ranges for meristic features are presented first, followed by modal counts when data were sufficient.

Measurements less than 150 mm were taken to the nearest 0.1 mm with dial calipers or ocular micrometer. Measurements over 150 mm were taken to the nearest mm with a steel ruler. Measurements are expressed either as thousandths of standard length (SL) or thousandths of head length (HL).

Morphometric abbreviations

ABL anal fin length
BD body depth
CD chin depth
CFL caudal fin length
DBL dorsal fin length
ED eye diameter
HL head length
HW head width
LHL lower head lobe width
OPUL width of upper opercular lobe
OPLL width of lower opercular lobe
PA pelvic to anal fin length
PAL preanal length
PDL predorsal length
PL pelvic fin length
POL postorbital length
SNL snout length
UHL upper head lobe width
UJL upper jaw length

All descriptions of pigmentation are based on fishes fixed in formalin and stored in ethyl or isopropyl alcohol.

Maturity was estimated by macroscopic examination of stages of developing ova and extent of posterior elongation of the ovaries (ovaries of mature females are sometimes conspicuous through the body wall in transmitted light; in immature females and large females, ovaries are best observed by dissection). Since no obvious differences in male testicular size were apparent, estimates of maturity were based entirely on females. Immature females were those with nonelongate or only partially elongate ovaries. Mature females had fully elongate ovaries. Gravid females were those individuals with enlarged ovaries filled with large, macroscopically visible ova.

When available, depth-of-capture information (converted to the nearest meter) was recorded and summarized for specimens listed in the "Material examined" sections in each species account. If depth of capture included a range of depths over which the nets were towed, a mean depth for that particular trawl was calculated.

Synonomies are selective for *S. plagusia* and *S. tessellatus* because of the numerous locality citations; synonomies are presumed to be complete for the other species. Because of their common occurrence, *S. plagusia* and *S. tessellatus* are listed in numerous studies, beginning with the oldest literature dealing with shallow-water marine fish faunas of the Caribbean and temperate regions of eastern South America. Since little descriptive or ecological information was provided in most original accounts of these tonguefishes, it is often impossible, when reviewing the literature, to determine accurately the species studied. For example, in studies of tonguefishes occurring in the Caribbean and along the coasts of Central and northern

South America, the possibility exists of any combination of four species being considered in the accounts. Since many of these earliest studies of Caribbean fishes considered only shore-zone fishes, much of this literature is discussed under the account of *S. plagusia*, one of the more widely distributed shallow-water species, and the one first named in the complex. Most references from extreme southern South America pertaining to shallow-water tonguefishes possessing 12 caudal fin rays refer to *S. tessellatus* and are included in the synonymy of that species. Synonymies for the remaining species include only those studies from which I examined specimens.

Abbreviations of institutions

Institutions providing study material, or in which type material is deposited are:

ALA Museum of Natural History, University of Alabama, University
ANSP Academy of Natural Sciences, Philadelphia
BMNH British Museum of Natural History, London
CAS-SU California Academy of Sciences, San Francisco
FMNH Field Museum of Natural History, Chicago
GCRL Gulf Coast Research Laboratory, Ocean Springs
IMS Marine Sciences Institute, University of Texas at Austin, Port Aransas
LACM Natural History Museum of Los Angeles County, Los Angeles
MCP Museu de Ciencias, Pontificia Universidade Catolica do Rio Grande do Sul, Porto Alegre
MCZ Museum of Comparative Zoology, Harvard University, Cambridge
MHNN Musee d'Histoire Naturelle de Neuchâtel, Neuchâtel
MNHN Museum National d'Histoire Naturelle, Paris
TCWC Texas Cooperative Wildlife Collection, Texas A&M University, College Station
TU Department of Zoology, Tulane University, New Orleans
UF Florida State Museum, University of Florida, Gainesville
UFPB Departamento de Sistematica e Ecologia, Universidade Federal da Paraiba, Joao Pessoa
UMML Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami
UMMZ Museum of Zoology, University of Michigan, Ann Arbor
UPRM University of Puerto Rico at Mayaguez
USA University of South Alabama, Mobile
USNM National Museum of Natural History, Smithsonian Institution, Washington, DC
ZMA Zoologisch Museum, Universiteit van Amsterdam

Artificial key to Western Atlantic members of the *Symphurus plagusia* complex

1a Large black spot on outer margin of ocular-side opercle; dorsal fin rays 91–107; anal fin rays 77–89; total vertebrae 50–55 ..... **2**

1b No obvious black spot on ocular-side opercle; dorsal fin rays 86–97; anal fin rays 70–81; total vertebrae 46–51 ..... **3**

2a 4–8 small ctenoid scales on blind side of posterior rays of dorsal and anal fins; ocular-side lower jaw without fleshy ridge on posterior portion; jaws reaching only to rear margin of pupil or rear margin of eye; crossbands wide, usually nine or less; posterior third of dorsal and anal fins without alternating series of pigment blotches and unpigmented areas, usually becoming increasingly darker posteriorly (black in mature males); dorsal fin rays 91–102; anal fin rays 77–86; total vertebrae usually 50–53. (Caribbean Sea to Uruguay) ..... ***S. tessellatus* (Quoy and Gaimard)**

2b No ctenoid scales on blind side of posterior rays of dorsal and anal fins; ocular-side lower jaw usually with pronounced fleshy ridge on posterior portion; jaws reaching rear margin of lower eye or extending slightly posterior to rear margin of lower eye; crossbands narrow, usually 10–14; dorsal and anal fins with alternating series of blotches and unpigmented areas, usually not becoming darker posteriorly; dorsal fin rays 99–106; anal fin rays 81–88; total vertebrae usually 53–54. (Guyana to northern Brazil) ..... ***S. oculellus* new species**

3a Dorsal and anal fins with an alternating series of dark blotches and unpigmented areas; ocular-side lower jaw without fleshy ridge on posterior portion; snout pointed; distance between upper eye and dorsal fin base usually slightly smaller than twice eye diameter; body with 9–15, narrow, dark crossbands; eye usually 9.0–10.0% of HL. (Caribbean Sea) ..... ***S. caribbeanus* new species**

3b Dorsal and anal fins usually uniformly pigmented, without obvious pigmented blotches; ocular-side lower jaw usually with pronounced fleshy ridge on posterior portion; snout squarish; distance from upper eye to dorsal fin base usually larger than twice eye diameter; body uniformly colored or with 4–9 faint crossbands; eye 6.4–11.0% HL, usually only 6.4–9.4% HL **4**

4a Eye usually only 6.4–9.5% HL; total vertebrae 49–51; dorsal fin rays 91–97; anal fin rays 75–81; longitudinal scales 79–89. (Caribbean Sea to southern Brazil) .... ***S. plagusia* (Schneider, in Bloch and Schneider)**

4b Eye 7.0–11.0% HL, usually 8.0–10.0% HL; total vertebrae usually 47–49; dorsal fin rays 86–93; anal fin rays 70–78; longitudinal scales 66–83. (Gulf of Mexico and southeastern United States) ..... ***S. civitatium* Ginsburg**

Table 1

Frequency distributions of predominant patterns of interdigitation of dorsal pterygiophores and neural spines (ID pattern) observed in five western Atlantic species of the *Symphurus plagusia* complex.

	ID pattern						
Species	1-3-3	1-3-4	1-4-2	1-4-3	1-4-4	1-5-2	1-5-3
civitatium	8	6	19	127	–	7	3
plagusia	4	1	2	32	1	–	1
tessellatus	10	16	11	177	12	3	14
oculellus	1	2	1	33	–	–	1
caribbeanus	8	3	–	69	2	2	

Table 2

Frequency distributions of the numbers of caudal fin rays for five western Atlantic species of the *Symphurus plagusia* complex.

	Caudal fin ray count			
Species	10	11	12	13
civitatium		8	163	
plagusia		2	39	1
tessellatus	4	11	216	2
oculellus		4	49	
caribbeanus	1	2	80	1

Table 3

Frequency distributions of the numbers of dorsal fin rays for five western Atlantic species of the *Symphurus plagusia* complex.

	Dorsal fin ray number																					
Species	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	$\bar{x}$
civitatium	2	3	14	33	49	46	23	1														90.1
plagusia				1	–	4	11	12	4	4	5	1										93.2
tessellatus						2	2	6	16	40	30	53	36	28	19	9	1					96.9
oculellus														4	14	17	9	5	2	–	1	101.2
caribbeanus				1	–	1	13	29	25	10	5											93.5

Table 4

Frequency distributions of the numbers of anal fin rays for five western Atlantic species of the *Symphurus plagusia* complex.

	Anal fin ray number																					
Species	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	$\bar{x}$
civitatium	1	2	6	34	49	57	20	3	1													74.3
plagusia				1	–	5	8	15	5	6	1	1										77.0
tessellatus								5	24	36	45	45	37	26	18	3	1					80.8
oculellus												1	2	5	17	17	5	5	1	2		84.8
caribbeanus					1	3	6	24	40	6	3											77.6

Table 5

Frequency distributions of the numbers of total vertebrae for five western Atlantic species of the *Symphurus plagusia* complex.

	Vertebrae number										
Species	46	47	48	49	50	51	52	53	54	55	$\bar{x}$
civitatium	2	34	108	28	2						48.0
plagusia		1	4	20	12	5					49.4
tessellatus				3	47	87	71	32	2		51.4
oculellus							2	23	11	1	53.3
caribbeanus			1	43	33	4					49.5

Table 6

Frequency distributions of the numbers of longitudinal scale rows for five western Atlantic species of the *Symphurus plagusia* complex.

	Scale rows																						
Species	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	$\bar{x}$
civitatium	1	—	—	—	2	—	—	1	4	8	11	5	14	8	7	3	3	1							77.2
plagusia														1	3	2	3	2	2	1	3	—	—	2	83.3
caribbeanus													3	—	4	11	4	3	6	2	2	1	1	3	82.8

	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	$\bar{x}$
tessellatus	2	2	8	10	10	11	21	31	21	21	14	5	4	2	—	1		87.9
oculellus				1	3	1	7	5	2	6	4	2	—	1	—	—	1	89.8

Table 7

Frequencies of the numbers of scale rows between the posterior margin of the eyes to the midpoint emargination of the opercle for five western Atlantic species of the *Symphurus plagusia* complex.

	Scale rows								
Species	16	17	18	19	20	21	22	23	$\bar{x}$
civitatium	3	18	32	16	3				18.0
plagusia			8	4	8	2	1		19.3
tessellatus			1	—	8	9	4	1	20.8
oculellus				3	8	1	1	2	20.4
caribbeanus		1	1	9	16	8	3		20.0

Table 8

Frequency distributions of the transverse scale count observed for five western Atlantic species of the *Symphurus plagusia* complex.

	Scale count																				
Species	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	$\bar{x}$
civitatium	2	1	2	—	2	5	4	6	2	11	5	6	6	1							33.9
plagusia										1	—	—	2	3	7	3	3	1			40.0
tessellatus													1	2	4	5	3	1	3	2	41.5
oculellus											1	1	6	2	2	1	1				38.7
caribbeanus											2	3	6	10	3	6	2	1	1		39.4

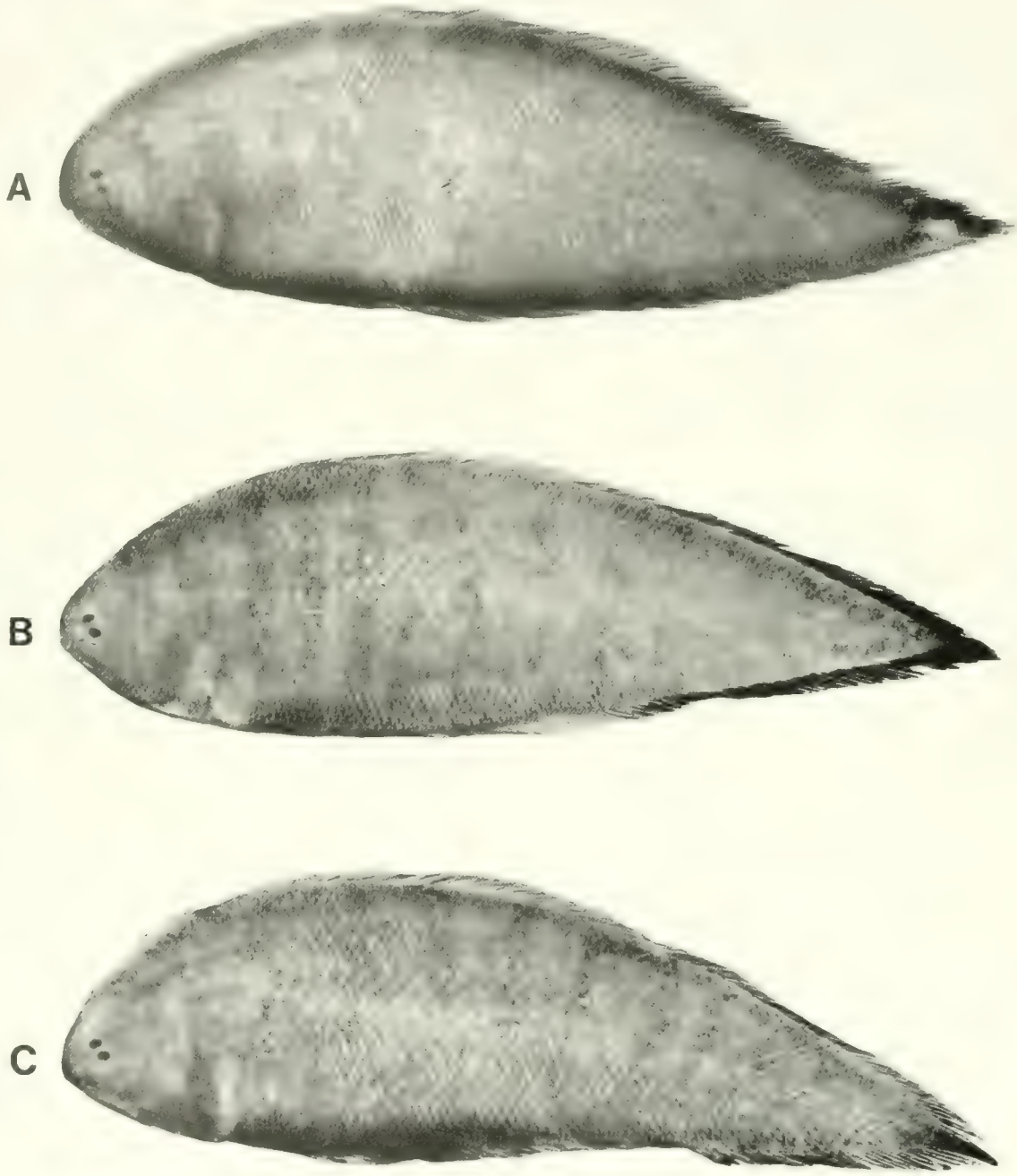


Figure 1

(A) *Symphurus plagusia*, Neotype, ANSP 132030, Female, 103.2 mm SL, Puerto Yabucoa, Puerto Rico. (B–C) *Symphurus civitatium*, FMNH 46369, Gulf of Mexico, 19°48′N, 91°20′W. (B) Male, 130 mm SL; (C) Female, 133 mm SL.

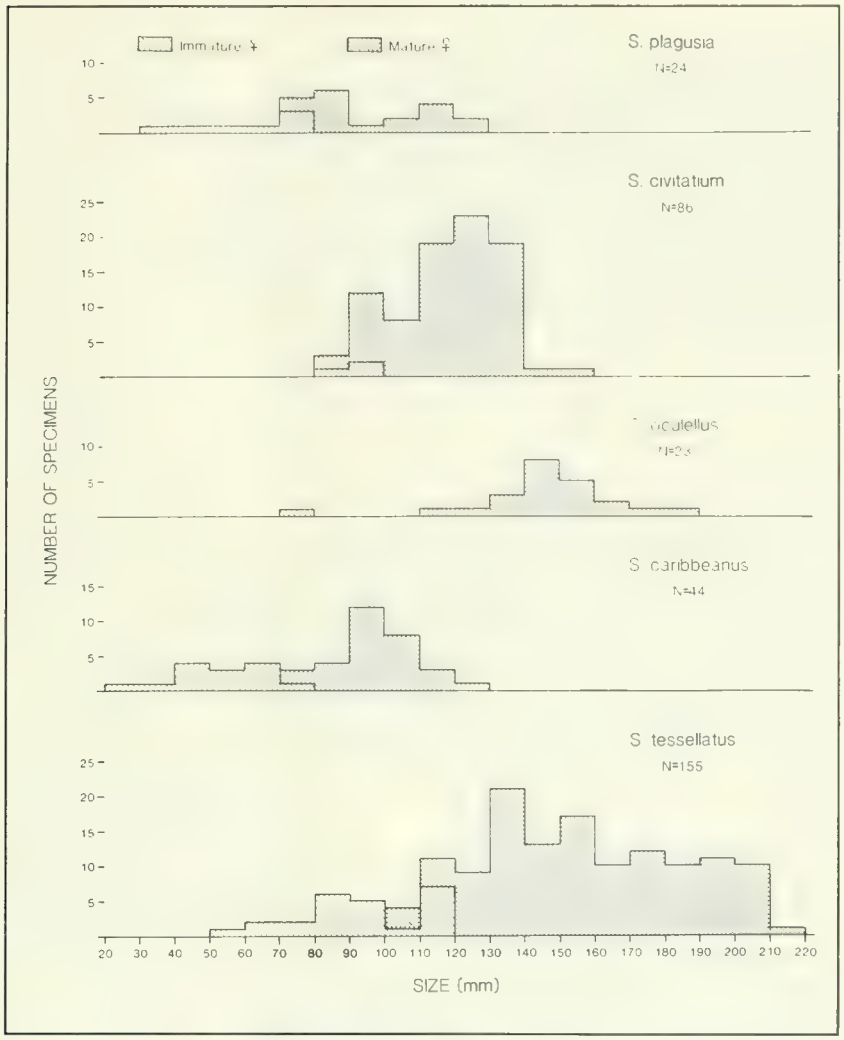


Figure 2
Frequency histogram of size distributions (standard length) and relative sizes at sexual maturity for females of five western Atlantic species of the *Symphurus plagusia* complex. Mature females were those with fully elongate ovaries. Immature females were those with non-elongate or only partially elongate ovaries.

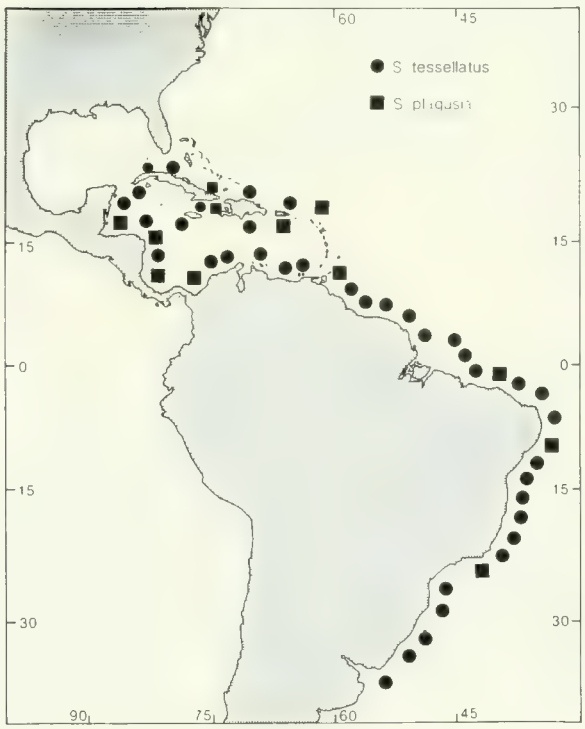


Figure 3
Geographic distributions of *Symphurus plagusia* and *S. tessellatus* based on material examined.

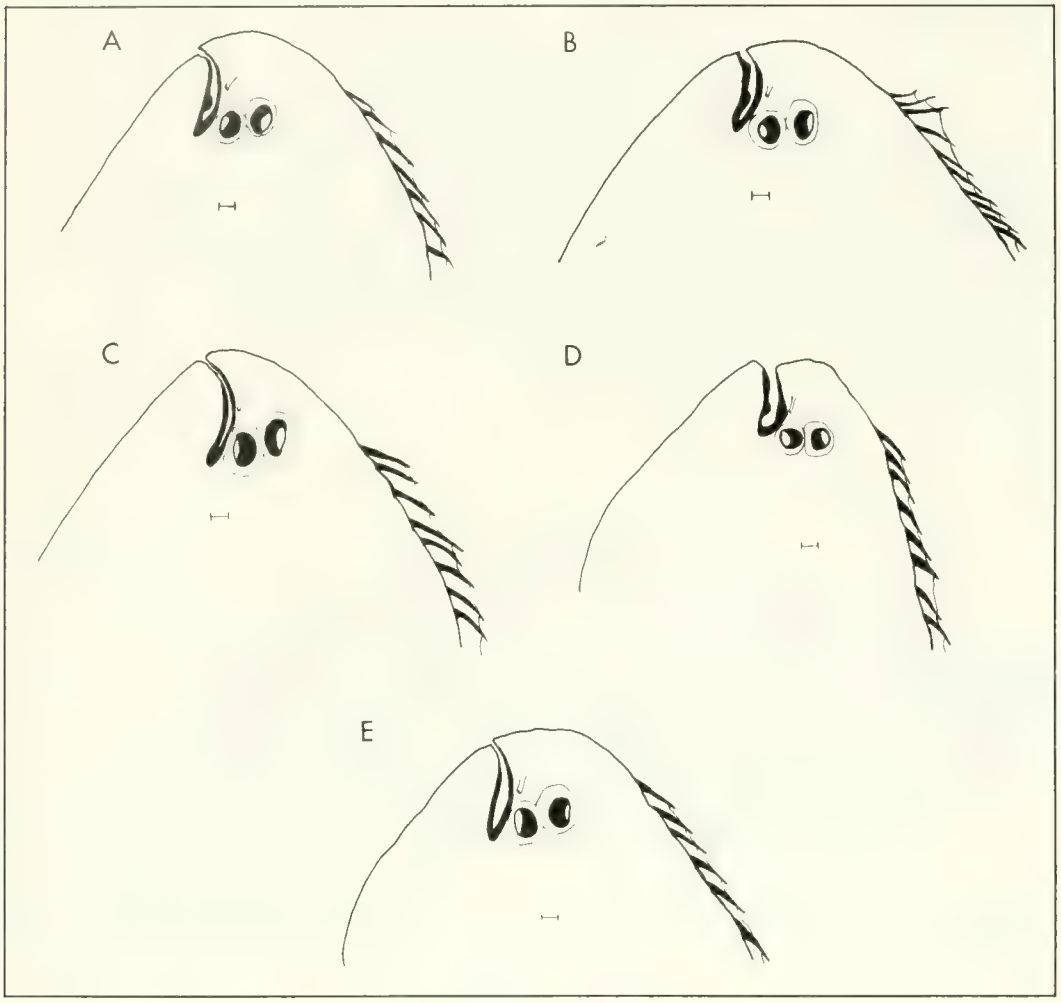


Figure 4
Schematic illustration of ocular-side lower jaws, head shapes, and relative positions of the dorsal fin origin for five western Atlantic tonguefishes of the *Symphurus plagusia* species complex. (A) *S. plagusia*, ANSP 132030. (B) *S. civitatium*, USNM 274485. (C) *S. tessellatus*, UPRM 2859. (D) *S. oculellus*, UMML 34334. (E) *S. caribbeanus*, USNM 313487. Bar = 1 mm.

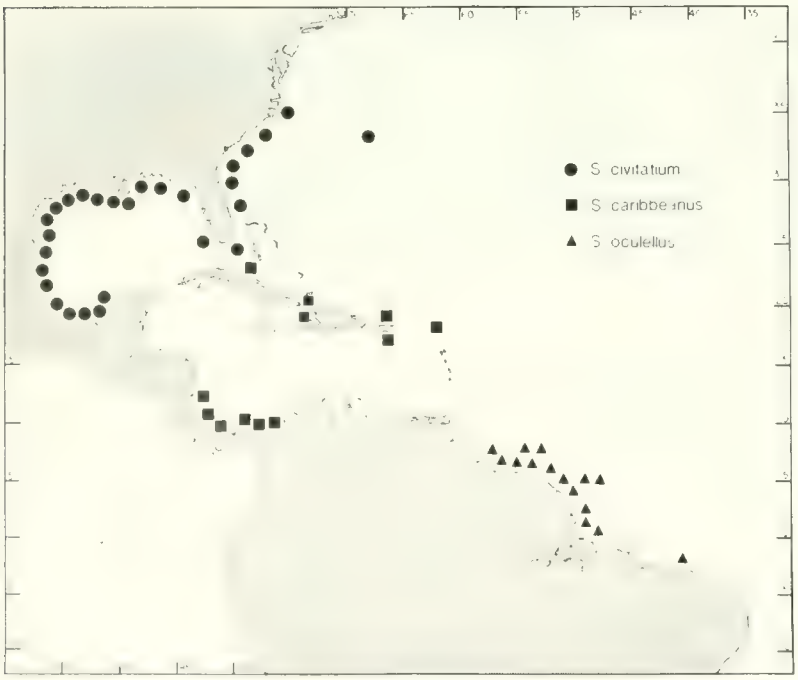
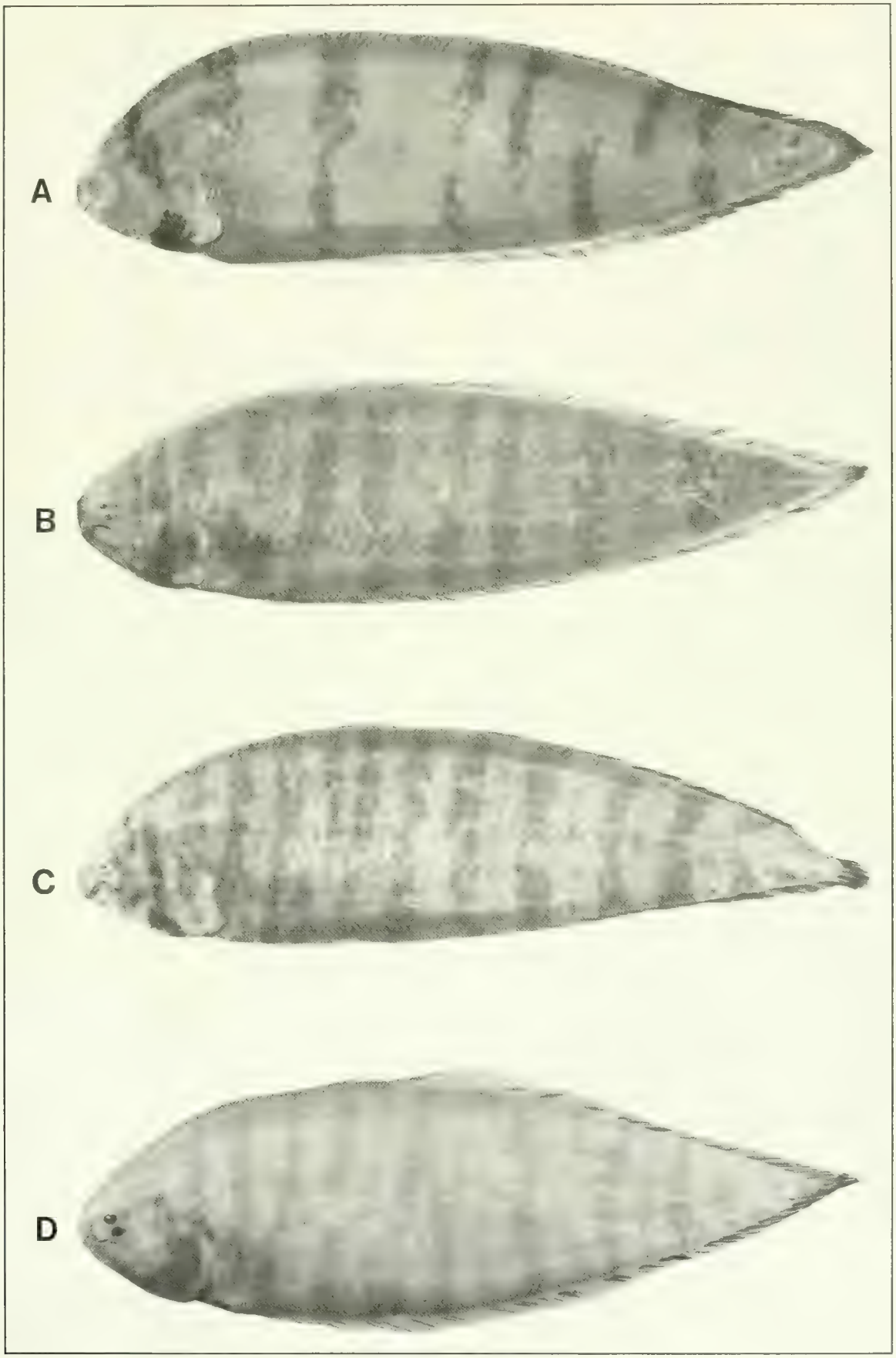


Figure 5
Geographic distributions of *Symphurus civitatium*, *S. oculellus*, and *S. caribbeanus* based on material examined.

Figure 6 (facing page)
(A) *Symphurus tessellatus*, USNM 159536, Female, 177 mm SL, Surinam, 6°41′N, 54°17′ W. (B–C) *Symphurus oculellus*. (B) Holotype, USNM 159606, 144 mm SL, Male, 6°24′N, 55°00′W; (C) USNM 313515, 151 mm SL, Female, 6°21′N, 54°28′W. (D) *Symphurus caribbeanus*, Holotype, USNM 313487, 101 mm SL, Male, Mayaguez Bay, Puerto Rico.


A
B
C
D

Systematics

Symphurus plagusia (Schneider, in Bloch and Schneider 1801) Figures 1a, 2, 3, 4a

Synonymy

Plagusia Browne 1756 (Jamaica; non-binomial; suppressed (Opinion 89 [Hemming and Noakes 1958:9], Plenary Powers for nomenclatorial purposes, Direction 32. Published 17 May 1956).

Pleuronectes plagusia Browne 1789:445 (Jamaica; non-binomial; suppressed (Opinion 89 [Hemming and Noakes 1958:9], Plenary Powers for nomenclatorial purposes, Direction 32. Published 17 May 1956). Cuvier 1816:224 (listed). Cuvier 1829:344 (listed).

Pleuronectes plagusia Schneider, in Bloch and Schneider 1801:162 (after Browne; no original material examined, based strictly on description provided by Browne).

?*Achirus ornata* (*nomen dubium*) Lacepède 1802:659, 663 (vague description of a tonguefish donated to France by Holland but of uncertain identity and geographic origin).

Aphoristia ornata. Kaup 1858:107 (in part) (new combination; synonymized with *Plagusia tessellata* Quoy and Gaimard 1824). Günther 1862:490 (in part) (synonymy; meristics; synonymized with *Plagusia tessellata* Quoy and Gaimard 1824). Poey 1868:409 (in part) (synonymy; listed, Cuba). Poey 1876:182 (in part) (synonymy; listed, Cuba). Goode and Bean 1885:196 (in part) (substitute name for *Pleuronectes plagiusa* Linnaeus 1766). Jordan 1885:395 (in part) (possible synonymy of *A. ornata* Lacepède 1802 with *Pleuronectes plagiusa* Linnaeus 1766; *Aphoristia ornata* Lacepède 1802 from Jamaica distinct from *A. fasciata* [= *Plagusia fasciata*] Holbrook in DeKay 1842).

Aphoristia plagiusa (not of Linnaeus). Jordan 1886a: 31 (Cuba; equals *A. ornata* of Poey). Jordan 1886b: 603 (in part) (West Indies; equals *A. ornata* of Poey).

Symphurus plagusia. Jordan and Goss 1889:100 (in part) (synonymy, nomenclature review; West Indies to Brazil; comparison with *S. plagiusa*; synonymized with *Plagusia tessellata* Quoy and Gaimard 1824). Jordan and Evermann 1898:2709 (in part) (synonymy, counts, measurements, description; after Jordan and Goss). Meek and Hildebrand 1928:1005 (in part) (synonymy; counts, measurements, description; summary of distribution records; listed, Panama). Chabanaud 1939:26 (listed, Antilles). Chabanaud 1940: 182 (descriptive osteology). Chabanaud 1949:82 (synonymy; description including counts, measurements, description of scales; figures; radiograph; mouth of Amazon, Brazil). Duarte-Bello and Buesa 1973:234 (in part) (synonymy; listed, Cuba). Menezes and Benvegnú 1976:142 (in part) (recommended reexamination of Ginsburg's diagnoses of two subspecies). Rosa 1980:222 (in part) (listed, nearshore and estuarine habitats, Paraiba, Brazil). Lema et al. 1980:44 (in part) (synonymy; listed, southern Brazil).

Symphurus plagusia plagusia. Ginsburg 1951:199 (in part) (synonymized with *Plagusia tessellata* Quoy and Gaimard 1824; description and diagnoses of two subspecies; four species included in material studied). Carvalho et al. 1968:22 (in part) (brief description; in key; Antilles, Central America to Brazil). Palacio 1974:87 (in part) (counts; suggested reexamination of subspecies status; listed, Colombia). Lema and Oliveira 1977:6 (in key; suggested synonymy of *Pleuronectes plagusia*, *Plagusia tessellata*, and *Symphurus civitatium*). Soares 1978:23 (in part) (listed, northern Brazil).

Diagnosis A *Symphurus* with the following combination of characters: predominant ID pattern 1-4-3; 12 caudal fin rays; unpigmented peritoneum; fleshy ridge on ocular-side lower jaw; no pupillary operculum; relatively small, spherical eye (64–95 HL, $\bar{x}$ 82); 89–97 dorsal fin rays; 73–81 anal fin rays; 47–51, usually 49–50, total vertebrae; 79–89 scales in longitudinal series; moderately long jaws, usually extending posteriorly to vertical line through posterior margin of lower eye, less frequently to vertical through rear margin of pupil or slightly posterior to rear margin of lower eye; dorsal fin origin placed far forward, usually at vertical through anterior margin of upper eye, or with first and sometimes second rays inserting anterior to vertical through anterior margin of upper eye; scales absent on blind sides of dorsal and anal fin rays; ocular surface usually uniformly light-brown or yellowish, occasionally with 8–14 narrow, faint crossbands; outer surface of ocular-side opercle without black blotch, pigmentation usually same as that of body (some specimens with dusky blotch on upper opercular lobe as a consequence of pigment on inner lining of ocular-side opercle showing through to outer surface); inner lining of ocular-side opercle and isthmus dusky- to dark-brown, that of blind side usually unpigmented or occasionally with small patch of pepper-dot pigmentation on ventral margin. Dorsal and anal fins uniformly pigmented, without progressive darkening or alternating series of pigmented blotches and unpigmented areas posteriorly.

Description A medium-sized tonguefish attaining maximum known body sizes of approximately 130 mm SL. ID pattern usually 1-4-3 (32/42 individuals), less frequently 1-3-3 (4), 1-4-2 (2), or 1-3-4 (1) (Table 1). Caudal fin rays 12(39/42), infrequently 11 or 13 (Table

Table 9

Summary of morphometrics, expressed as thousandths of standard length (except SL in mm) for the neotype (ANSP 132030) and 14 non-type specimens of *Symphurus plagusia*. (Abbreviations defined in Methods section.)

Character	Neotype	Range	Mean	SD
SL	103.2	57.4–130.3	98.8	22.29
BD	304	278–319	292.1	13.05
PDL	30	23–50	32.9	6.87
PAL	222	166–244	209.3	18.60
DBL	970	950–977	967.1	6.87
ABL	776	758–802	785.6	15.38
PL	64	51–73	63.6	5.76
PA	48	38–60	50.0	7.00
CFL	98	88–111	100.3	7.13
HL	196	174–216	189.6	11.98
HW	239	218–256	236.4	13.25
POL	130	110–143	125.9	9.26
SNL	45	36–54	43.3	4.21
UJL	42	38–52	43.1	4.56
ED	16	12–18	15.3	2.02
CD	42	39–67	52.1	7.99
UHL	142	125–186	160.1	15.93
LHL	107	81–115	96.8	10.22

Table 10

Summary of morphometrics expressed as thousandths of head length (except HL and HW) for the neotype (ANSP 132030) and 14 non-type specimens of *Symphurus plagusia*. (Abbreviations defined in Methods section.)

Character	Neotype	Range	Mean	SD
HL/HW	1.2	1.2–1.3	1.2	0.38
POL	663	630–714	665.8	25.18
SNL	228	205–250	229.1	15.62
UJL	213	200–250	227.6	14.99
ED	79	64–95	81.9	9.57
CD	213	222–374	275.1	40.32
OPLL	272	250–346	296.9	29.10
OPUL	223	169–272	211.9	27.24
UHL	703	695–926	843.1	63.80
LHL	530	427–606	510.3	53.23

2). Dorsal fin rays 89–97 (Table 3). Anal fin rays 73–81 (Table 4). Total vertebrae 47–51, usually 49–50 (32/42 specimens) (Table 5); abdominal vertebrae 3+6. Hypurals 4. Longitudinal scale rows 79–89 (Table 6). Scale rows on head posterior to lower orbit 18–22, usually 18–20 (Table 7). Transverse scales 35–43 (Table 8).

Proportional measurements appear in Tables 9 and 10. Body relatively deep (278–319 SL, $\bar{x}$ 292); maximum depth in anterior one-third of body. Preanal length 166–244 SL, $\bar{x}$ 209; shorter than body depth. Head relatively short (174–216 SL, $\bar{x}$ 190) and wide (HW 218–256 SL, $\bar{x}$ 236); usually much wider than long (HW/HL 1.2–1.3, $\bar{x}$ 1.2); lower head lobe relatively narrow (81–115 SL, $\bar{x}$ 97) considerably narrower than upper head lobe (125–186 SL, $\bar{x}$ 160). Lower opercular lobe of ocular side considerably wider (250–346 HL, $\bar{x}$ 297) than upper opercular lobe (169–272 HL, $\bar{x}$ 212). Postorbital length 110–143 SL, $\bar{x}$ 126. Snout moderately long (205–250 HL, $\bar{x}$ 229), somewhat square (Fig. 4a), covered with small ctenoid scales. Anterior nostril not reaching anterior margin of lower eye when depressed posteriorly. Dermal papillae well developed on blind side of snout and chin regions. Jaws moderately long, upper jaw length 200–250 HL, $\bar{x}$ 228; posterior extension of maxilla usually reaching to vertical line through posterior margin of lower eye, less frequently only to vertical through rear margin of pupil or slightly posterior to rear margin of lower eye. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin (Fig. 4a). Chin depth 222–374 HL, $\bar{x}$ 275. Lower eye small (64–95 HL, $\bar{x}$ 82), spherical; upper eye usually anterior to lower eye; eyes not covered with scales; usually 1–2 small ctenoid scales in narrow interorbital space. Pupillary operculum absent. Length of dorsal fin base 950–977 SL, $\bar{x}$ 967. Dorsal fin origin placed far forward (Fig. 4a), usually at vertical through anterior margin of upper eye or with first and sometimes second fin rays inserting anterior to vertical through anterior margin of upper eye; predorsal length 23–50 SL, $\bar{x}$ 33. Length of anal fin base 758–802 SL, $\bar{x}$ 786. Scales absent on blind sides of dorsal and anal fin rays. Pelvic fin length 51–73 SL, $\bar{x}$ 64; longest pelvic fin ray reaching base of first or occasionally second anal fin ray; pelvic to anal fin distance 38–60 SL, $\bar{x}$ 50. Posterior pelvic fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly almost to origin of anal fin base (membrane torn in many specimens). Caudal fin length moderate (88–111 SL, $\bar{x}$ 100).

Teeth well developed on blind-side jaws. Ocular-side dentary without teeth or with short row of small teeth developed only on anterior one-half to one-third; premaxilla on ocular side usually with small, single, mostly incomplete row of slender teeth anterior to vertical equal with anterior nostril.

Scales large, ctenoid on both sides of body.

Pigmentation Ocular surface usually uniformly light-brown or yellowish, occasionally with 8–14 narrow, faint crossbands. Crossbands not continued onto dorsal and anal fins; mostly complete in anterior trunk region; on remainder of body obvious only as vertical markings at body margin along dorsal and anal fin bases.

Table 11

Bathymetric distribution (meters) for five species of the western Atlantic *Symphurus plagusia* complex. Numbers represent the percent occurrence of individuals.

		Depth									
Species	*N*	1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	110
civitatium	216	2	26	34	26	5	5	0.5	0.5		
tessellatus	349	10	26	2	24	19	5	8	6	0.3	
oculellus	57	4	19	12	9	9	2	40	—	4	2
plagusia	25	80	—	—	16	—	—	4			
caribbeanus	94	51	32	17							

Blind side creamy-white. Peritoneum unpigmented. Pigmentation of outer surface of ocular-side opercle usually same as that of body; occasionally with dusky blotch on upper opercular lobe due to pigment on inner lining of ocular-side opercle showing through to outer surface. Inner lining of opercle and isthmus on ocular side usually dusky; some specimens with dark-brown pigmentation on inner opercular lining; inner opercle and isthmus on blind side usually unpigmented or occasionally with small patch of pepper-dot pigmentation on ventral margin. Usually with slight pigment band on ocular-side upper lip and diffuse pattern of melanophores on lower lip.

Dorsal and anal fins dusky; fin rays streaked with pigment darker brown than that of connecting membrane; sometimes with alternating series of darker-pigmented rays (usually 2–3 in succession) separated by about 4–5 successive, lighter-pigmented rays. Basal half (scale-covered) of caudal fin dark-brown; fin rays in distal half streaked with pigment.

Size and sexual maturation (Fig. 2) *Symphurus plagusia* is a medium-sized tonguefish. The largest of five males examined was 130 mm SL; the largest of 23 females was only slightly smaller (127 mm SL).

Sexual maturity occurs at a relatively large body size in this species. All females larger than 80 mm SL were mature. All but one female (79.3 mm SL) smaller than 80 mm SL were immature, with gonads undergoing elongation without ripening ova or with ovaries barely elongating.

Geographic distribution (Fig. 3) Widely distributed in shallow waters of the tropical western Atlantic. In the northern portion of its distribution, this species occurs in Puerto Rico, Haiti, and Hispaniola, but is unknown from the Bahamas (Böhlke and Chaplin 1968). Along the continental margin of Central America, *S. plagusia* has been collected at Belize, Nicaragua, Costa Rica, and Panama, while further south it ranges along the Atlantic coast of Colombia and coastal regions in Surinam, Tobago, and Brazil at least as far south as Rio de Janeiro.

Bathymetric distribution *Symphurus plagusia* is a shallow-water species (1–51 m) most commonly inhabiting depths between the shoreline and 10 m (Table 11), where (20/25, 80%) of specimens examined were taken. All life-history stages occur in these shallow areas and only occasionally were individuals taken at deeper locations (one specimen at 51 m, three specimens at 40 m, and one specimen at 37 m).

Ecology Little is known concerning the biology of *S. plagusia*. Its general rarity in collections indicates that it occurs in rarely-sampled habitats.

Remarks The earliest description of a western Atlantic, shallow-water, 12-caudal-rayed tonguefish is of a specimen collected in Jamaica that Browne first described (1756) as *Plagusia* and later (1789) as *Pleuronectes plagusia*. He described this specimen as a small sinistral flatfish with dorsal, anal, and caudal fins united (tail ending in sharp point), lacking pectoral fins and lateral lines. His description was clearly that of a tonguefish, but he provided no figure or diagnostic characters to unequivocally identify his specimen. Browne's names were later suppressed under the plenary powers for nomenclatorial purposes in Opinion 89 of the Commission for Zoological Nomenclature (see Hemming and Noakes 1958).

In 1801, Schneider first made Browne's tonguefish *Pleuronectes plagusia* available as a binomial. Schneider's *Pleuronectes plagusia* was based entirely on the description of the tonguefish from Jamaica in Browne's works (1756, 1789). The description by Schneider (in Bloch and Schneider 1801) is identical to that provided by Browne and, in addition, all indications are that Schneider did not directly examine any specimens of this species. Dr. H.-J. Paepke (Mus. für Naturkunde der Humboldt-Universität zu Berlin, Zoologisches Mus., Invalidenstrasse 43, Berlin DDR 1040, pers.

commun. 8 Nov. 1986) informs me that no remarks were made in Bloch's ledger to indicate that specimens were available for examination when Schneider wrote the description of *Pleuronectes plagusia*. Additionally, Paepke also stated that there are no specimens of this species in the Bloch and Schneider collection. Therefore, it appears that the description of *Pleuronectes plagusia* Schneider, in Bloch and Schneider 1801, was copied directly from Browne's work and that no type exists for this species.

Although quite vague, the original description of *Pleuronectes plagusia* by Schneider does refer to a species of *Symphurus* and is the oldest available name for a tropical, western Atlantic species in the genus. This name represents the oldest binomial generally considered to represent a member of this species group and has been the one name most consistently applied to any shallow-water tonguefish possessing 12 caudal fin rays. In order to stabilize the nomenclature for this species, it is necessary to designate a neotype. Since the original description is based on a specimen from Jamaica, a topotypic specimen would be the most appropriate neotype. Unfortunately, no specimens of *S. plagusia* from Jamaica were available to Munroe (1987) and several more recent attempts to procure a specimen during the present study have also been unsuccessful. All tonguefishes collected from Jamaican waters that I have examined are specimens of *S. tessellatus* trawled at depths generally exceeding those usually occupied by *S. plagusia*. Therefore, designation of a neotype for *S. plagusia*, based on a topotype specimen from Jamaica, is not possible. Instead, ANSP 132030, a mature female measuring 103.2 mm SL, collected by beach seine at Puerto Yabucoa, Puerto Rico, 24–27 July 1974, is selected as the neotype for this species. Meristic features for this specimen are: ID pattern 1-4-3; caudal fin rays 12; dorsal fin rays 93; anal fin rays 78; total vertebrae 50; longitudinal scales 79; transverse scale count 39; and 18 scale rows on head posterior to eyes.

Many authors have included *Achirus ornatus* Lacepède 1802 in the synonymy of *Symphurus plagusia*. The description of this species is very brief and does not include figures or locality data, and it is unknown if any type(s) exists. The information provided is that the fish was donated to France by Holland, and has the following characteristics: dorsal and anal fins joined, 95 dorsal fin rays, 82 anal fin rays, 8 or 9 dark transverse bands, and a lateral line on each side. Notably absent in Lacepède's account is the caudal-fin-ray count for this specimen. The lateral line referred to in the description may refer to the mid-lateral junction of the myomeres that is apparent on some tonguefish specimens (especially those partially dehydrated during preservation). Based on counts listed by Lacepède, it is possible his specimen is a *S. plagusia* (*sensu strictu*). However, the dark, transverse bands and meristic features listed in the description of *Achirus ornatus* could also apply to several other western Atlantic tonguefishes. Among shallow-water species possessing 12 caudal fin rays, the data fit at least three species: *S. caribbeanus* (described below), *S. plagusia* (Schneider, in Bloch and Schneider 1801), and *S. tessellatus* (Quoy and Gaimard 1824). Of these, the description is more typical of *S. tessellatus*, especially the reference to darkly-pigmented crossbands. Nonetheless, the exact identity of *Achirus ornatus* Lacepède cannot be determined from the vague original description, particularly given the unknown site of capture for the specimen on which this name is based. *Achirus ornatus* Lacepède 1802 is therefore regarded as a *nomen dubium*.

In 1824, Quoy and Gaimard described *Plagusia tessellata* from Rio de Janeiro Bay (= Guanabara Bay), Brazil. Although no figure of this specimen was provided, the descriptive account of meristic features, color pattern, and other characters leave little doubt as to the identity of the species. Quoy and Gaimard described the dorsal fin as originating above the eyes and consisting of 99 rays; the anal fin has 78 rays. The color is described as brown with small transverse bands of the same color. Although no type exists for this species (M.L. Bauchot, Ichtyologie Générale et Appliquée, 43 Cuvier, Mus. Natl. Hist. Nat., Paris Cedex 05 75231, pers. commun. 23 June 1982), the original description is sufficient to allow identification of this species. Unfortunately, most authors beginning with Kaup (1858) and continuing to Ginsburg (1951) regarded this species as a junior synonym of *S. plagusia* (Schneider, in Bloch and Schneider 1801). It is unlikely that the specimen described by Quoy and Gaimard belongs to *S. plagusia* (*sensu strictu*), because the *S. tessellatus* specimen has slightly higher meristic features, darker banding, and the dorsal fin origin is described as being above and not anterior to the eyes, which is the typical condition found in *S. plagusia*.

A second nominal species of tonguefish from Brazilian waters, *Plagusia brasiliensis*, described by Agassiz (in Spix and Agassiz 1829–1831), has also been placed in the synonymy of *S. plagusia*. The possible holotype or syntype (MHNN 691; see Kottelat 1984, 1988) was illustrated and an adequate description provided. The specimen has 99 dorsal fin rays, 83 anal fin rays, 12 caudal fin rays, 53 total vertebrae, several small ctenoid scales on the blind sides of the dorsal and anal fin rays, the dorsal fin origin at the vertical through the front margin of the pupil of the upper eye, and a relatively large eye (10.6% HL). It agrees in all these features with *S. tessellatus* and is removed from the synonymy

of *S. plagusia* and placed in the synonymy of *S. tessellatus* (see below).

Beginning with Kaup (1858), all previously described species of western Atlantic, shallow-water tonguefishes possessing 12 caudal fin rays were regarded as a single species. Kaup placed *Achirus ornatus* Lacepède, *Plagusia brasiliensis* Agassiz, in Spix and Agassiz (Kaup cited authorship of this species as Cuvier, in Spix), and *Plagusia tessellatus* Quoy and Gaimard (Kaup listed Valenciennes as the author of this name) in synonymy and proposed the new combination *Aphoristia ornata* to accommodate a single, widespread species ranging from the Caribbean to southern South America. Günther (1862) regarded *Aphoristia ornata* as including the nominal species *Pleuronectes plagusia* Browne, *Plagusia brasiliensis* Agassiz, and *Plagusia tessellatus* Quoy and Gaimard.

Subsequent authors, including Jordan and Goss (1889) and Jordan and Evermann (1898), until Ginsburg (1951), continued to include three species in the synonymy of *Symphurus* (= *Aphoristia*) *plagusia* (Schneider, in Bloch and Schneider): *P. tessellatus*, *P. brasiliensis*, and *A. ornatus*. Jordan and his co-workers, and other researchers, still recognized only one widespread, polytypic species of shallow-water, 12-caudal-rayed *Symphurus* occurring in the western Atlantic. Ginsburg (1951), although continuing to regard all Caribbean and South American specimens as representing a single widespread, polytypic species, *S. plagusia* (Schneider, in Bloch and Schneider 1801), allocated his study specimens to two allopatric subspecies. He considered *S. plagusia plagusia* as a northern subspecies ranging from the West Indies to Central America that was characterized by somewhat lower meristic features. The second subspecies, *S. p. tessellatus*, with a more southern distribution along the coasts of Brazil and Uruguay had higher meristic features. In this revision, Ginsburg also described a second species (*S. civitatum* = *civitatium*, this study) of shallow-water, 12-caudal-rayed tonguefish from continental seas off the southeastern United States and Gulf of Mexico. He equivocated in his description of this new species, stating that his *S. civitatium* could also be recognized as a third northern subspecies of a widespread, polytypic *S. plagusia*.

Subsequent workers have utilized subspecies designations proposed by Ginsburg for Caribbean and South American shallow-water, 12-caudal-rayed tonguefishes and have used the name *S. civitatium* for specimens collected in the Gulf of Mexico and along the southeastern coast of the United States. More recently, however, several studies have noted that both nominal subspecies of *S. plagusia* occur sympatrically in northern South America. For example, Carvalho et al. (1968) found both subspecies in northern Brazil, and Palacio (1974) reported both subspecies from the Colombian Caribbean.

In their revision of western South Atlantic tonguefishes, Menezes and Benvegnú (1976) reported that all their specimens (collected mostly in offshore habitats by trawling) were quite similar, lacking variation reported for specimens collected in more northern regions. Using the name *S. plagusia*, they considered their specimens to represent a single taxon but also pointed out that the sympatric occurrence of both subspecies in other South American localities indicated that the subspecific status designated by Ginsburg should be reexamined.

In examining material of *S. plagusia*, I successfully located 19 of the 25 specimens listed by Ginsburg (1951) in his account of *S. plagusia plagusia*. These include representatives of four species: twelve *S. tessellatus*, one *S. caribbeanus*, one *S. parvus* Ginsburg 1951, with only five actually *S. plagusia* (*sensu strictu*). The twelve specimens of *S. tessellatus* incorrectly identified as *S. p. plagusia* by Ginsburg are small juveniles collected from shallow-water habitats. These, as well as many of the remaining 25 specimens that Ginsburg included in his account of *S. p. plagusia*, had been collected in the latter part of the last century and during the early 1920s. Most of these older specimens were completely devoid of any obvious pigmentation pattern. As a consequence, the specimens provided little clue that more than a single species was represented in these shallow-water collections. Additionally, since most of Ginsburg's Caribbean and Central American specimens came from shallow-water collections, very few adult *S. tessellatus* were available to his study. Therefore, he was unable to unravel size-related differences among the three sympatric species in this complex that occur in this region (the two smaller species, *S. plagusia* and *S. caribbeanus*, and the much larger *S. tessellatus*).

Ginsburg did not list catalog numbers for 34 specimens identified as *S. p. tessellatus* in his study, so that it is difficult to ascertain if more than one species was included in his account of this subspecies. Of the eight lots designated as *S. p. tessellatus* by Ginsburg that I have examined, all are one species, *S. tessellatus* (Quoy and Gaimard 1824). It is highly probable, therefore, that Ginsburg's *S. p. tessellatus* are equivalent to *S. tessellatus* (Quoy and Gaimard 1824) in the present study.

Comparisons *Symphurus plagusia* most closely resembles *S. civitatium* but differs from that species in its modally higher meristic features (total vertebrae modally 49–50 vs. 47–49 in *S. civitatium*; dorsal fin rays 89–97 vs. 86–93; anal fin rays 73–81 vs. 70–78); and degree of development of sexually dimorphic coloration. In *S. plagusia*, both sexes are more or less

uniformly pigmented with only slight evidence of banding on the body, and with vertical fins of both sexes uniformly colored with no darkening in the posterior portion of the body. In contrast, in *S. civitatium* there is considerably more pronounced sexual dimorphism in pigmentation. Females tend to have well-developed crossbands on the body whereas in males the crossbands are less conspicuous. In male *S. civitatium*, posterior portions of the dorsal and anal fins are noticeably darkened with black pigment (black pigment absent in females).

Symphurus plagusia of all sizes are usually collected with juveniles and small adults of *S. tessellatus*. Despite overall similarities in meristic features, the two species are quite distinctive. *Symphurus plagusia* is uniformly colored with only faint, narrow crossbands in some individuals, has a well-developed fleshy ridge on the ocular-side lower jaw (Fig. 4a), and this species lacks a striking black pigment spot on the outer opercle (some individuals have a diffuse blotch on the inner opercle where the pigmentation on the inner surface of the ocular-side opercle shows through). In *S. tessellatus*, in contrast, all individuals have a bold pattern of wide crossbands, a prominent black spot on the outer surface of the opercle, and lack a fleshy ridge on the ocular-side lower jaw (Fig. 4c). *Symphurus plagusia* also has a smaller eye (6.4–9.5, $\bar{x}$ 8.2% HL vs. 7.9–11.4, $\bar{x}$ 9.5% HL in *S. tessellatus*) and lacks the small ctenoid scales on the posterior fin rays on the blind side of the dorsal and anal fins that are present in *S. tessellatus* larger than about 70 mm SL. *Symphurus plagusia* also has modally lower meristic values (total vertebrae 49–50 vs. 50–53 in *S. tessellatus*; dorsal fin rays 89–97 vs. 91–102 (usually 93–101); anal fin rays 73–81 vs. 77–86 in *S. tessellatus*).

Symphurus plagusia differs further from *S. tessellatus* in the almost squarish snout of *S. plagusia*, which contrasts with the more pointed snout of *S. tessellatus* (compare Figs. 4a and 4c). Also, in *S. plagusia* the dorsal fin origin is usually anterior to the vertical through the eye, while in *S. tessellatus* the dorsal fin originates slightly more posteriorly, usually above the anterior margin of the pupil of the upper eye, or even as far back posteriorly as the mid-eye region. Viewed from the blind side, the more posterior location of the dorsal fin origin in *S. tessellatus* is apparent in the number of rays occurring along the dorsal margin of the body immediately above the space between the two nostrils. In *S. tessellatus* usually only the first dorsal fin ray occurs above the space between the nostrils, while the second dorsal fin ray lies immediately above the posterior nostril or the second dorsal fin ray is placed even slightly posterior to the rear nostril. In *S. plagusia*, usually the first two dorsal fin rays occur along the dorsal margin in the space between the nostrils, and in many specimens the first dorsal fin ray is actually situated anterior to the vertical equal with the anterior nostril. In *S. plagusia*, the jaws usually extend to the posterior margin of the lower eye or, in some cases, actually extend slightly posterior to the rear margin of the lower eye, while in *S. tessellatus* the jaws usually reach only to the middle, rarely to the posterior margin, of the lower eye.

These two species also differ significantly in overall body size and size at sexual maturation. *Symphurus plagusia* is a medium-sized tonguefish reaching a maximum known body size of about 130 mm SL and attaining sexual maturity as small as 80 mm SL. *Symphurus tessellatus* is a much larger species attaining maximum known lengths of 220 mm SL and does not attain sexual maturity until reaching approximately 120 mm SL.

Meristic values of *S. plagusia* overlap almost completely those of *S. caribbeanus*. The two species can be distinguished, however, by the absence in *S. caribbeanus* of the fleshy ridge on the ocular-side lower jaw (present in *S. plagusia*; see Figures 4a and 4e). *Symphurus plagusia* is generally uniformly colored with only slight evidence of crossbanding, and the fins are uniformly colored. In contrast, *S. caribbeanus* usually has numerous, prominent crossbands on the body, and the vertical fins have an alternating series of blotches and unpigmented areas, which are especially well developed posteriorly. *Symphurus caribbeanus* has a more pointed snout with a distance between upper eye and dorsal fin base usually slightly less than twice the eye diameter, versus a squarish snout with distance from upper eye to dorsal fin base usually larger than twice the eye diameter in *S. plagusia* (compare Figures 4a and 4e). The body shape of *S. caribbeanus* is rounded with a pronounced taper posterior to dorsal fin rays 25–35 (versus somewhat elongate in *S. plagusia* with a more gradual taper). Additionally, *S. caribbeanus* has a slightly larger eye (8.2–11.0% HL, usually 9.0–10.0% HL) when compared with that of *S. plagusia* (usually 7.0–9.0% HL).

Symphurus plagusia is also similar to *S. oculellus* with respect to small eye size and presence of a fleshy ridge on the ocular-side lower jaw. It differs from this species, however, in its much lower counts (47–51 total vertebrae vs. 52–55 in *S. oculellus*; dorsal fin rays 89–97 vs. 99–104; anal fin rays 73–81 vs. 82–88) and pigmentation pattern. *Symphurus plagusia* has a relatively uniform body color with faint crossbands, uniformly pigmented fins without blotches, and no pigment spot on the outer opercle (versus sharply contrasting crossbands, pigmented blotches alternating with unpigmented areas in the dorsal and anal fins, and a black spot on the outer opercle in *S. oculellus*). Furthermore, in *S. plagusia* the first, and occasionally the second, rays of the dorsal fin are usually located along

a vertical line anterior to the upper eye, while in *S. oculellus* the dorsal fin origin usually extends anteriorly only to the vertical through the anterior margin or mid-eye region of the upper eye. Differences in morphometrics between the two species are that *S. oculellus* has a narrower body (231–297 SL vs. 278–319 SL in *S. plagusia*) and attains larger sizes (up to 190 mm SL vs. largest of only 131 mm SL in *S. plagusia*).

Some meristic values of *S. plagusia* overlap those of 11 other species of Atlantic tonguefishes. *Symphurus plagusia* occurs sympatrically, and occasionally syntopically, with *S. diomedeanus* (Goode and Bean) but differs from this species in having 12 caudal fin rays (versus 10 in *S. diomedeanus*) and in lacking the series of dark spots on posterior rays of the dorsal and anal fins and the pupillary operculum that are present in *S. diomedeanus*.

Symphurus plagusia can be distinguished from *S. plagiusa* (Linnaeus), which has an allopatric distribution in the western North Atlantic, in having 12 versus 10 caudal fin rays, and *S. plagusia* also lacks the well-developed black pigment spot on the ocular-side outer opercle (present in *S. plagiusa*). In addition, only the ocular-side opercular lining is pigmented in *S. plagusia* whereas the inner opercular linings on both sides of the body are heavily pigmented in *S. plagiusa*. *Symphurus plagiusa* has larger eyes (83–126 HL vs. 64–95 HL in *S. plagusia*) that are usually equal in position (slightly subequal in *S. plagusia*). Also, in *S. plagiusa* the jaws reach only as far posteriorly as a vertical through the mid-eye region; in contrast, in *S. plagusia* the jaws reach a vertical through the rear margin of the pupil or the rear margin of the eye, or the jaws occasionally even extend slightly beyond the vertical through the posterior margin of the lower eye in *S. plagusia*. In larger (>60 mm SL) *S. plagiusa*, there are 4–8 ctenoid scales on the blind sides of the dorsal and anal fin rays (scales usually absent altogether, or occasionally 1–2 scales along bases of fin rays in *S. plagusia*).

Symphurus plagusia is not easily confused with other Atlantic species (*S. kyaropterygium* Menezes and Benvegnú, *S. trewavasae* Chabanaud, *S. normani* Chabanaud, *S. piger* (Goode and Bean), *S. nigrescens* Rafinesque, *S. pusillus* (Goode and Bean), *S. lubbocki* Munroe, and *S. reticulatus* Munroe) with which it overlaps in meristic features. *Symphurus plagusia* differs from all of these in its 1-4-3 ID pattern (versus 1-4-2 in *S. kyaropterygium*; 1-3-3 in *S. trewavasae* and *S. normani*; 1-3-2 in *S. piger*, *S. nigrescens*, *S. pusillus*, *S. reticulatus*, and *S. lubbocki*). In addition, *S. plagusia* differs from the South Atlantic *S. kyaropterygium* in caudal-fin-ray number (12 vs. 10) and in lacking the pupillary operculum and dark pigment blotch on the caudal extremity that are present in *S. kyaropterygium*. It differs from the South Atlantic *S. trewavasae* in its caudal-fin-ray count (12 vs. 10) and smaller eye (64–95 HL vs. 114–162 HL in *S. trewavasae*). *Symphurus plagusia* lacks scales on the blind sides of the dorsal and anal fin rays and the spotted peritoneum that are present in *S. normani*. *Symphurus plagusia* differs from the 1-3-2 species (except *S. lubbocki* and *S. reticulatus*) in lacking a black peritoneum. *Symphurus plagusia* differs from *S. lubbocki* and *S. reticulatus* in having no dentition or greatly reduced dentition on ocular-side jaws (versus ocular-side jaws with complete or nearly complete row of teeth in *S. lubbocki* and *S. reticulatus*), its much larger size (130 vs. <50 mm SL), and pigmentation (dark- or light-brown, usually without crossbands, and with uniformly-pigmented fins, versus light-brown or yellowish body with incomplete crossbands in *S. lubbocki*, and dark, chocolate-brown body with X- and Y-shaped markings and vertical fins with alternating series of blotches and unpigmented areas in *S. reticulatus*).

Meristic values of *S. plagusia* overlap those of six eastern Pacific species possessing either a 1-4-3 or 1-5-3 ID pattern, including *S. leei* Jordan and Bollman, *S. atricaudus* (Jordan and Gilbert), *S. melanurus* Clark, *S. williamsi* Jordan and Culver, *S. fasciolaris* Gilbert, and *S. melasmatotheca* Munroe and Nizinski. Of these species, *S. plagusia* is most similar to *S. melanurus* in that both species possess a fleshy ridge on the ocular-side lower jaw, and in both the first dorsal fin ray reaches a vertical equal with or anterior to the anterior margin of the upper eye. The two species are distinguished in that *S. plagusia* lacks a pupillary operculum (versus a weakly-developed pupillary operculum usually present in *S. melanurus*), has fewer scales in a longitudinal series (79–89 vs. 89–108 in *S. melanurus*), has a lightly-pigmented inner lining on the blind-side opercle (versus darkly-pigmented inner lining on the blind-side opercle in *S. melanurus*), and in *S. plagusia* the posterior dorsal and anal fins and the caudal fin are not darker than the anterior regions (versus progressive darkening in posterior dorsal and anal fins and darkly-pigmented caudal fin in *S. melanurus*). *Symphurus plagusia* differs from the remaining five eastern Pacific species with comparable meristic values in lacking a pupillary operculum (present in the others) and in having a fleshy ridge on the ocular-side lower jaw (absent in the others). *Symphurus plagusia* is further distinguished from *S. fasciolaris* and *S. melasmatotheca* in possessing 12 caudal fin rays (versus 10 and 11 in *S. fasciolaris* and *S. melasmatotheca*, respectively) and in lacking an ocellated spot on the caudal fin (present in *S. fasciolaris*) or pigmented peritoneum (present in *S. melasmatotheca*). *Symphurus plagusia* differs further from *S. atricaudus* and *S. williamsi* in lacking small ctenoid scales on the blind sides of the dorsal and anal fin rays (present in these other species).

From *S. leei*, *S. plagusia* is further distinguished in having the head length considerably smaller than the head width (versus head length usually equal to or greater than head width in *S. leei*), in having a smaller eye (12–18 SL vs. 22–27 SL in *S. leei*), and in having an unpigmented peritoneum (versus black or heavily spotted in *S. leei*).

Material examined 45 specimens (19.5–130 mm SL).

Counted and measured (15 specimens, 57.4–130.3 mm SL) **Puerto Rico**: ANSP 132030; Neotype; (102.9); Puerto Yabucoa, one-half mile east of Playa de Guayanes, Municipio de Yabucoa; collected by J.J. Loos, 24–27 Jul 1973. FMNH 3286; (83.1); Mayaguez; 20 Jan 1899. FMNH 61572; (117.0); Allasco Bay; 10 Jan 1954. UF 12059; (127.1); beach at Mani, just N of Mayaguez; 16 Apr 1964. **Costa Rica**: UF 10762; (79.6); Tortuguero Lagoon, Limon Province; Aug 1963. **Panama**: GCRL 15694; (57.4); Canal Zone; 8 Feb 1977. **Trinidad**: UPRM 1828; (89.4); Icacos Bay; 4 May 1964. **Brazil**: FMNH 88853; 2(120.0–130.3); 2°09′S, 42°44′W; 40 m; 10 Mar 1963. UFPB 884; (101.4); Praiade Jacare; 13 Nov 1981. UFPB 896; 3(79.3–87.5); Rio Paraiba do Norte; 30 Jul 1981. ANSP 121326; 2(112.9–118.3); Atafona (23°02′S, 44°01′W); Jul–Aug 1963.

Counted (27 specimens, 17 lots) **Puerto Rico**: ANSP 118542; (47.4); Puerto Yabucoa; 25 Jan 1971. ANSP 129952; (112.7); Puerto Yabucoa; 21 Jul 1973. ANSP 129985; (98.2); Puerto Yabucoa; 25 Jul 1973. USNM 50178; 4(61.9–83.1); Ponce; 31 Jan 1899. **Haiti**: UF 33896; 5(82.8–90.8); 2 km NW of Port Salut; sandy beach near eelgrass bed; 7 Apr 1979. **Belize**: FMNH 97492; (49.3); Belizean Beach, 4.5 mi on Western Highway; 16 Apr 1973. FMNH 97493; 2(52.1–68.2); Belizean Beach, 4.5 mi on Western Highway; 16 Apr 1973. FMNH 97494; (25.1); Belize City, St. John's College Beach; 16 Apr 1973. FMNH 97495; (36.4); Belize City, St. John's College Beach, mangroves and beach; 3 Aug 1973. **Honduras**: FMNH 94818; (54.3); Brus Lagoon; 1 m; 10 May 1975. FMNH 94822; (34.8); Roatan; 1 m; 1 May 1975. FMNH 97490; 3(19.5–61.3); Stann Creek District, along Pelican Beach, 17–33 m N of Pelican Beach Motel; 30 Mar 1973. FMNH 97491; (40.0); Stann Creek District, along Pelican Beach, 17–33 m N of Pelican Beach Motel; 15 Apr 1973. **Panama**: UMML 34347; (121.5); 7°42′N, 57°32′W; 27 m; 15 Jul 1968. USNM 81654; (54.9); Colon; 5 Jan 1911. **French Guiana**: USNM 236252; (110.5); 6°34′N, 54°28′W; 37 m; 28 Jun 1972. USNM 291331; (79.4); 5°30′N, 52°10′W; 51 m; 12 Sep 1958.

Other material examined (3 specimens, 1 lot) **Tobago**: USNM 313648; 3(19.5–20.3); Bloody Bay, 11°18′14″N, 60°37′46″W; 3 m; 13 Sep 1990.

Symphurus civitatium Ginsburg 1951
Figures 1b–c, 2, 4b

Synonymy

Symphurus piger (not of Goode and Bean). Baughman 1950:137 (inner harbor, Freeport, Texas).

Symphurus civitatum Ginsburg 1951:198 (counts, figure, included in key; Gulf of Mexico and southeastern coasts of the United States; see "Remarks" about emendation of specific name). Springer and Bullis 1956:65 (Gulf of Mexico; list of *Oregon* stations at which this species was collected). Resén-dez 1979:646 (occurrence in lagunas El Carmen, La Machona, and Lagunade Terminos, northern Mexico).

Symphurus civitatus. Briggs 1958:297 (summary of distribution records; North Carolina to Florida and widespread in Gulf of Mexico; see "Remarks" about emendation of specific name). Roithmayr 1965:22 (included in industrial bottomfish catch in north-central Gulf of Mexico). Struhsaker 1969:298 (rarely occurring [<10% of the tows] in demersal fish community of continental shelf from North Carolina to central Florida). Swingle 1971:65 (listed, offshore waters of Alabama). Topp and Hoff 1972:78 (general absence from west Florida shelf). Miller and Jorgenson 1973:305 (meristic features reported for four specimens). Chittenden and McEachran 1976: 93; 99 (abundance on continental shelf of northwestern Gulf of Mexico). Walls 1976:390 (counts, figure, in key; suggested synonymy with *S. plagiusa*). Schwartz et al. 1981:32 (Cape Fear River, North Carolina). McCaffrey 1981:204 (in part) (abundance and distribution in northeastern Gulf of Mexico). Darcy and Gutherz 1984:104 (collected on west Florida continental shelf).

Diagnosis *Symphurus civitatium* is identified by the combination of: a predominant 1-4-3 ID pattern; 12 caudal fin rays; an unpigmented peritoneum; absence of a pupillary operculum; relatively small eye (70–110 HL, $\bar{x}$ 88); a fleshy ridge on the ocular-side lower jaw; 86–93 dorsal fin rays; 70–78 anal fin rays; 46–50, usually 47–49 total vertebrae; 66–83, usually 74–82, scales in longitudinal series; relatively short jaws usually extending posteriorly to a vertical line through the middle of the pupil of the lower eye, or sometimes extending to the vertical line through the posterior margin of the pupil of the lower eye; dorsal fin origin usually situated at the vertical anterior to the front margin of the upper eye, or occasionally only reaching the vertical line through the front margin of the pupil of the upper eye; scales usually absent on the blind sides of the dorsal and anal fin rays (occasionally with 1–3 small scales at proximal bases of fin rays but without scales on distal portions of fin rays); ocular surface

usually light- to dark-brown, occasionally with 6–14 narrow, dark-brown crossbands; outer surface of ocular-side opercle without black blotch, pigmentation usually same as that of body (some specimens with dusky blotch on upper opercular lobe as a consequence of pigment on inner lining of ocular-side opercle showing through to outer surface); inner lining of ocular-side opercle and isthmus usually heavily pigmented, that of blind side usually unpigmented. Dorsal and anal fins considerably darker posteriorly, without an alternating series of pigmented blotches and unpigmented areas.

Description A medium-sized tonguefish reaching maximum lengths of approximately 152 mm SL. The usual ID pattern (Table 1) is 1-4-3 (127/177 specimens), less frequently 1-4-2 (19/177) and 1-5-2 (7/177). Caudal fin rays usually 12 (163/171), infrequently 11 (Table 2). Dorsal fin rays 86–93 (Table 3). Anal fin rays 70–78 (Table 4). Total vertebrae 46–50, usually 47–49 (170/174) (Table 5); abdominal vertebrae 3 + 6. Hypurals 4. Longitudinal scale rows 66–83, usually 74–82 (Table 6). Scale rows on head posterior to lower orbit 16–20, usually 17–19 (Table 7). Transverse scales 26–39, usually 31–38 (Table 8).

Proportional measurements appear in Tables 12 and 13. Body relatively deep (247–328 SL, $\bar{x}$ 307) with greatest depth in anterior one-third of body. Preanal length 147–238 SL, $\bar{x}$ 202. Head moderately short, 170–219 SL, $\bar{x}$ 191; considerably shorter than body depth. Head wide (212–271 SL, $\bar{x}$ 238); usually greater than head length (HW/HL 1.0–1.5, $\bar{x}$ 1.2); lower head lobe (87–118 SL, $\bar{x}$ 104) narrower than upper head lobe (139–184 SL, $\bar{x}$ 159). Lower opercular lobe of ocular side (253–388 HL, $\bar{x}$ 321) considerably wider than upper opercular lobe (178–329 HL, $\bar{x}$ 230). Postorbital length 117–187 SL, $\bar{x}$ 134. Snout relatively short (169–231 HL, $\bar{x}$ 206), somewhat square (Fig. 4b); covered with small ctenoid scales. Anterior nostril, when depressed posteriorly, not reaching anterior margin of lower eye. Dermal papillae well developed on blind side of snout and chin regions. Jaws relatively short; upper jaw length 181–289 HL, $\bar{x}$ 228; posterior extension of maxilla usually reaching to vertical line through middle of pupil of lower eye or sometimes to vertical through posterior margin of pupil of lower eye. Chin depth 225–331 HL, $\bar{x}$ 268. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin (Fig. 4b). Lower eye relatively small (70–110 HL, $\bar{x}$ 88); upper eye slightly anterior to lower eye; eyes not covered with scales; usually only 1–3 small ctenoid scales in narrow interorbital space. Pupillary operculum absent. Length of dorsal fin base 925–982 SL, $\bar{x}$ 963. Dorsal fin origin (Fig. 4b) usually situated at vertical line anterior to front margin of upper eye; occasionally dorsal fin origin only reaching vertical line through front margin of pupil of upper eye; predorsal length 22–46 SL, $\bar{x}$ 34. Scales usually absent on blind sides of dorsal and anal fin rays; occasionally with 1–3 small scales at proximal bases of fin rays but without scales on distal portions of fin rays. Pelvic fin length 49–85 SL, $\bar{x}$ 63; longest pelvic fin ray usually reaching base of first or occasionally second anal fin ray; pelvic to anal fin distance 33–74 SL, $\bar{x}$ 45. Posteriormost pelvic fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly almost to origin of anal fin base (membrane torn in most specimens). Caudal fin relatively short, 87–124 SL, $\bar{x}$ 109.

Table 12
Summary of morphometrics expressed in thousandths of standard length, except SL (in mm), for the holotype (USNM 155227) and 29 additional specimens of *Symphurus civitatium*. (Abbreviations defined in Methods section.)

Character	Holotype	*N*	Range	Mean	SD
SL	110.3	30	48.8–149.3	108.6	24.96
BD	304	30	247–328	306.9	16.42
PDL	43	29	22–46	34.5	6.78
PAL	210	30	147–238	202.4	19.75
DBL	957	30	925–982	963.0	13.22
ABL	787	30	745–891	797.9	31.36
PL	68	30	49–85	63.0	8.83
PA	39	26	33–74	44.7	10.23
CFL	124	29	87–124	108.6	9.32
HL	200	30	170–219	191.3	11.55
HW	240	30	212–271	238.3	14.42
POL	134	30	117–187	134.3	13.64
SNL	41	30	31–47	39.5	3.55
UJL	54	30	37–54	43.5	4.88
ED	16	30	13–21	16.6	2.01
CD	62	29	39–68	50.6	7.32
UHL	159	30	139–184	158.9	11.60
LHL	103	30	87–118	103.9	6.86

Teeth well developed on blind-side jaws. Dentary on ocular side with single, mostly incomplete row of slender teeth on anterior one-third of jaw. Premaxilla on ocular side with only short row of teeth on anterior one-third; or occasionally lacking teeth altogether.

Scales large, ctenoid on both sides of body.

Pigmentation Body coloration generally similar for both sexes (dichromatic differences in pigmentation are discussed below). Ocular surface light- to dark-brown; sometimes with dark-brown crossbands continuous across the body. Crossbands, when developed, narrow, 6–14 in number, sometimes sharply contrasting (especially in mature females), otherwise faint and barely perceptible against dark body coloration. Crossbands not continued onto dorsal and anal fins. First band

Table 13
Summary of morphometrics expressed in thousandths of head length (except HW/HL) for the holotype (USNM 155227) and 29 additional specimens of *Symphurus civitatium*. (Abbreviations defined in Methods section.)

Character	Holotype	*N*	Range	Mean	SD
HW/HL	1.2	30	1.0–1.5	1.2	0.10
POL	670	30	645–740	692.0	27.45
SNL	204	30	169–231	206.4	13.84
UJL	272	30	181–289	227.7	24.14
ED	81	30	70–110	87.8	10.26
CD	308	29	225–331	267.9	30.55
OPLL	371	29	253–388	321.3	34.80
OPUL	217	29	178–329	230.0	34.86
UHL	792	30	636–996	832.6	82.14
LHL	516	30	462–629	543.0	46.00

crossing head short distance anterior to opercular opening. Crossbands along trunk 3–6 scale rows wide. Two posteriormost bands immediately anterior to caudal fin base often conjoined. Blind side off-white. Peritoneum unpigmented. Dorsal margin of outer surface of ocular-side opercle often with dusky blotch due to dark pigmentation of inner lining of opercle showing through to outer surface. Inner lining of opercle and isthmus on ocular side usually heavily pigmented; lining of blind-side opercle and blind-side isthmus usually unpigmented. Band of pigmentation usually developed on ocular-side upper lip; lower lip on ocular side frequently spotted but usually without definite band.

Pigmentation of dorsal and anal fins generally similar in both sexes, but usually more intense in males. All dorsal and anal fin rays on anterior two-thirds of body streaked with brown pigment similar in shade and intensity to body color. Fin rays completely pigmented other than for extreme distal tips, which are unpigmented. Membranes of anterior three-fourths of fins unpigmented. Caudal fin and dorsal and anal fins on posterior one-third of body more heavily pigmented and considerably darker than anterior two-thirds of fin. Fin membranes on posterior quarter of body heavily pigmented. Basal one-third of caudal fin more lightly pigmented than posterior two-thirds of fin. Distal tips of middle caudal fin rays unpigmented, or with tips of middle caudal fin rays streaked with pigment but membrane unpigmented.

Size and sexual maturity (Fig. 2) The largest fish examined, a female (152 mm SL), was only slightly larger than the largest male (149 mm SL). Most specimens examined ranged in size from 80 to 140 mm SL.

Females mature at sizes usually larger than 90 mm SL. Of 86 females examined, only three (83–95 mm SL) were immature. The two smallest gravid females were 80–90 mm SL, whereas the majority of gravid females were usually larger (91–140 mm SL).

Geographic distribution (Fig. 5) Western North Atlantic from Cape Hatteras, North Carolina, to the Yucatan Peninsula of Mexico. There is a single record for this species from Bermuda (ANSP 137573). In the Gulf of Mexico, *S. civitatium* occurs most commonly west of Apalachicola Bay in northern Florida (Springer and Bullis 1956, Chittenden and McEachran 1976, McCaffrey 1981). It is one of the most commonly collected tonguefishes on inner continental shelf regions in the central and western portions of the Gulf of Mexico from Alabama to Texas. Along northern Mexico, this species occurs coastally on sandy substrates at least as far south as coastal lagoons (lagunas El Carmen y La Machona, Laguna de Terminos) in Tabasco and Campeche, Mexico (Reséndez 1979) and on the continental shelf of the southern Gulf of Mexico (Cabo Rojo, Veracruz to Sabuncuy, Yucatan).

Collection data for 347 specimens from this study reveal a general absence of this species from the western Florida shelf. Only two collections record this species from the Tortugas region off southern Florida. Topp and Hoff (1972) also noted the general absence of this species along the west Florida shelf and found just a single record for *S. civitatium* in the eastern Gulf of Mexico (St. Joseph Bay; from Ginsburg 1951). Neither their efforts during the Hourglass cruises on the continental shelf off west Florida nor other studies (Moe and Martin 1965, Ogren and Brusher 1977, Naughton and Saloman 1978) have collected this species in coastal and continental shelf habitats off west Florida. Furthermore, Darcy and Gutherz (1984) reported taking only a single specimen during 338 10-minute bottom trawls in 9–193 m on the west Florida shelf.

Symphurus civitatium occurs on sand or silt substrates throughout its range. The geographic and bathymetric distribution of this species apparently coincides with the distribution of terrigenous, quartzite sandy, and silty substrates on the inner continental shelf. The scarcity of this species on the west Florida shelf and Yucatan Peninsula may reflect the strikingly different substrate compositions there. Along the west Florida shelf, primarily in depths of 55–92 m, Topp and Hoff (1972) reported that substrates consist of lithified sediments of cemented lime, including (1) nearshore deposits of cemented shell beachrock, (2) limestone, ranging from soft marl to conglomeritic and foraminiferal limestone, (3) small patches of living and dead coral, and (4) calcareous algae. They noted that substrates off the Yucatan Peninsula are similar in composition to those of the west Florida shelf. In

contrast, in the central and western Gulf of Mexico from the Mississippi Delta to Cabo Rojo, Veracruz, where *S. civitatium* is very abundant, substrates on the inner shelf consist largely of terrigenous quartzite sands, silts, and clays delivered primarily by Mississippi and Rio Grande rivers (van Andel 1960).

Substrate preference may also affect the distribution of *S. civitatium* in coastal seas off the southeastern United States. The depth of occurrence (11–40 m, see below) for *S. civitatium* apparently coincides with sand-silt substrates on the inner portions of the shelf, and this species is absent from live-bottom habitats occurring at similar depths (Struhsaker 1969).

The specimen of *S. civitatum* reported by Lazzaro (1977:69) from the continental shelf off Uruguay is neither this species nor any other of the *Symphurus plagusia* complex (those possessing 12 caudal fin rays, a 1-4-3 ID pattern, and an unpigmented peritoneum). The body shape evident in the photograph, meristic features, and great depth of occurrence (183 m) indicate the specimen is probably *S. ginsburgi* Menezes and Benvegnú.

Bathymetric distribution Although *S. civitatium* has been collected over a wide depth range of 1–73 m (Table 11), its center of abundance, based on overall frequency of capture and general abundance, occurs between 11 and 45 m. Approximately 91% (199/216) of the specimens examined in the present study were captured at these depths. The deepest captures were at 73 and 62 m, where a single fish was taken each time. It is unusual for adult *S. civitatium* to occur in shallow, inshore regions. Of four fish collected shallower than 10 m, three were small juveniles (<35 mm SL). Recently, several small juveniles (22–24 mm SL) have been collected in the Cape Fear River estuary, North Carolina (S.W. Ross, Dep. Nat. Resour., Morehead City, NC, pers. commun. 24 July 1985). It is not known how regularly this species occurs in these inshore areas or whether the recent captures represent isolated occurrences; however, Schwartz et al. (1981) listed this species as rare in the Cape Fear River estuary. Seasonal occurrence and abundance of juveniles in nearshore waters need further investigation.

McCaffrey (1981) reported capture depths of 30–187 m for 23 specimens purported to be *S. civitatium* taken on the continental shelf in the northeastern Gulf of Mexico between 84°30′ and 89°00′W longitudes. Nineteen of these specimens were collected between 80 and 187 m, depths considerably deeper than records for specimens I examined. Not all specimens identified as *S. civitatium* by McCaffrey were preserved and curated in collections (at least nine were indicated as having been discarded). One retained specimen (UF 70946) collected at 45 m, is *S. civitatium*, but two other specimens (UF 70885) from *Tursiops* Station 7019-07 with an estimated depth of 187 m are, rather, *S. pusillus* (Goode and Bean) and an undescribed species (species C of Munroe 1987), which occur commonly at depths similar to that reported for this station (187 m). Given the complexity of the series identified as *S. civitatium* in McCaffrey's study, the very deep captures reported (80–187 m) for *S. civitatium* are probably erroneous.

Remarks In the original description of *S. civitatum*, Ginsburg (1951:198) stated that this species and *S. plagusia* differed enough to consider them distinct species but that it was possible that they represented subspecies of a more widespread polytypic species. It was shown earlier (see "Remarks" section in account of *S. plagusia*) that Ginsburg had more than one species in his account of *S. plagusia*, and therefore his subspecific designations for this species were unfounded. *Symphurus civitatium* is consequently recognized as a species within this complex of morphologically similar species of *Symphurus*.

The etymology of the name *civitatum*, applied by Ginsburg to this species, is unclear from the original description. The name may have been derived from the genitive plural of *civitas* (meaning "of the citizenry"). Following this assumption, the proper genitive plural is *civitatium*, not *civitatum* as indicated by Ginsburg (G.C. Steyskal, Dep. Entomology, Natl. Mus. Nat. Hist., Wash. DC, pers. commun. 1989). Thus, the spelling of the specific name for this species remains unchanged regardless of generic assignment of the species. Therefore, spelling changes such as *S. civitatus* (Bailey et al. 1960, and other checklists of common and scientific names) are incorrect.

Comparisons *Symphurus civitatium* is most similar to, but has a completely allopatric distribution from, the Caribbean and South Atlantic species *S. plagusia*. Differences between these two species were discussed in the "Comparisons" section under the account for *S. plagusia*.

Meristic features of *S. civitatium* overlap at least partially those of two other Atlantic species belonging to this complex (the Caribbean and South Atlantic species *S. caribbeanus* and *S. tessellatus*). There is almost complete overlap in several meristic features between *S. civitatium* and *S. caribbeanus*; however, *S. civitatium* has a fleshy ridge on the ocular-side lower jaw (absent in *S. caribbeanus*; see Figures 4b and 4e) and has lower modal counts for total vertebrae (47–49 vs. 49–50 in *S. caribbeanus*), dorsal fin rays (86–93 vs. 89–96), and anal fin rays (70–78 vs. 74–80). *Symphurus civitatium* also has narrow crossbands with uniformly-colored fins (becoming progressively darker

in the posterior portions of sexually mature males). In contrast, *S. caribbeanus* has numerous well-developed crossbands and vertical fins with an alternating series of blotches and unpigmented areas in individuals of both sexes. *Symphurus caribbeanus* also has a more pointed snout with only a narrow space between the upper eye and dorsal fin base (versus a square snout with a space between the upper eye and the dorsal fin base usually greater than twice the eye diameter in *S. civitatium*; compare Figures 4b and 4e).

Despite some overlap in certain meristic values, *S. civitatium* and *S. tessellatus* are quite distinctive. The easiest way to distinguish these species is that *S. civitatium* has a well-developed fleshy ridge on the ocular-side lower jaw (absent in *S. tessellatus*; compare Figures 4b and 4c), lacks a black spot on the ocular-side opercle, and, when present on the body, crossbands are faint and narrow, whereas *S. tessellatus* has a bold pattern of wide crossbands and a well-developed black opercular spot. Other distinctions between these species include the absence of scales on the blind sides of the dorsal and anal fin rays of *S. civitatium* (present in *S. tessellatus* larger than about 60 mm SL), fewer vertebrae (total vertebrae 47–49 vs. 50–53 in *S. tessellatus*), and modally lower meristic features: dorsal fin rays 86–93 vs. 91–102 (usually 93–101) in *S. tessellatus*; anal fin rays 70–78 vs. 77–86; scales in a longitudinal series 66–83 vs. 81–96.

Some meristic values of *S. civitatium* overlap those of 11 other species of Atlantic tonguefishes. *Symphurus civitatium* occurs sympatrically with *S. diomedeanus* and *S. plagiusa* and may be collected with these species. The suggestion by Walls (1976:390) to synonymize *S. civitatium* with *S. plagiusa*, based on partial overlaps in meristic features, pigmentation, and ecological co-occurrence, is not supported by results of this study. *Symphurus civitatium* differs from both these species primarily in caudal-fin-ray count (12 vs. 10 in the others) and by notable differences in pigmentation patterns. *Symphurus diomedeanus* usually has a series of black spots on posterior rays of the dorsal and anal fins and a well-developed pupillary operculum (both characters absent in *S. civitatium*). *Symphurus civitatium* can be distinguished from *S. plagiusa* in that *S. plagiusa* usually has a well-developed black spot on the outer surface of the ocular-side opercle (absent altogether or only a diffuse blotch resulting from pigment from the inner opercular lining showing to the outside in *S. civitatium*), and inner opercular linings on both sides are heavily pigmented (only the ocular-side opercular lining is pigmented in *S. civitatium*). *Symphurus plagiusa* has larger eyes (83–126 HL) that are usually equal in position (versus smaller eyes 70–110 HL, which are slightly subequal in position in *S. civitatium*). Also, the jaws reach only as far posteriorly as a vertical through the mid-eye region in *S. plagiusa*, while in *S. civitatium* the jaws reach a vertical through the rear margin of the pupil, the rear margin of the eye, or may even extend slightly beyond a vertical equal with the posterior margin of the lower eye in *S. civitatium*. In larger *S. plagiusa*, there are 4–8 ctenoid scales on the blind sides of the dorsal and anal fin rays (absent or at most only 1–2 scales along bases of fin rays in *S. civitatium*).

Symphurus civitatium is not easily confused with other Atlantic species (*S. kyaropterygium*, *S. trewavasae*, *S. normani*, *S. piger*, *S. nigrescens*, *S. pusillus*, *S. lubbocki*, and *S. reticulatus*) with which it overlaps in some meristic features. *Symphurus civitatium* differs from all of these in ID pattern (1-4-3 versus other patterns: 1-4-2 in *S. kyaropterygium*; 1-3-3 in *S. trewavasae* and *S. normani*; 1-3-2 in *S. piger*, *S. nigrescens*, *S. pusillus*, *S. reticulatus*, and *S. lubbocki*). In addition to differences in ID pattern, *S. civitatium* differs from the South Atlantic *S. kyaropterygium* in caudal-fin-ray number (12 vs. 10) and in lacking the pupillary operculum and darkly-pigmented blotch on the caudal extremity both present in *S. kyaropterygium*. *Symphurus civitatium* differs from the South Atlantic *S. trewavasae* principally in caudal-fin-ray count (12 vs. 10) and its smaller eye (70–110 HL vs. 114–162 HL in *S. trewavasae*). The eastern Atlantic *S. normani* possesses scales on the blind sides of the dorsal and anal fin rays, has a spotted peritoneum, and pepper-dot pigmentation on the blind side of the body (all absent in *S. civitatium*). *Symphurus civitatium* differs from the species with a 1-3-2 ID pattern (except *S. lubbocki* and *S. reticulatus*) in lacking a black peritoneum. *Symphurus civitatium* is further distinguished from *S. lubbocki* and *S. reticulatus* in having a fleshy ridge on the ocular-side lower jaw (absent in these others), in lacking complete dentition on ocular-side jaws (ocular-side jaws without dentition, or with only a partial row of teeth, versus ocular-side jaws with complete dentition in *S. lubbocki* and *S. reticulatus*), by its much larger size (152 vs. <50 mm SL), and by differences in pigmentation (dark-brown body with crossbands and uniformly-pigmented fins versus light-brown or yellowish body with incomplete crossbands in *S. lubbocki* and dark chocolate-brown body with X- and Y-shaped markings and vertical fins with alternating series of blotches and unpigmented areas in *S. reticulatus*).

Meristic values of *S. civitatium* overlap those of five eastern Pacific species possessing either a 1-4-3 or 1-5-3 ID pattern, including *S. atricaudus*, *S. melanurus*, *S. williamsi*, *S. fasciolaris*, and *S. melasmatotheca*. Of these species, *S. civitatium* is most similar to *S. melanurus* in that both possess a fleshy ridge on the ocular-side lower jaw, and in both the first dorsal fin ray reaches the vertical equal with or anterior to the

anterior margin of the upper eye. The two species differ in that *S. civitatium* lacks a pupillary operculum (versus a weakly-developed pupillary operculum usually present in *S. melanurus*), has fewer scales in a longitudinal series (66–83 vs. 89–108 in *S. melanurus*), and *S. civitatium* has an unpigmented or only lightly-pigmented inner lining on the blind-side opercle (versus darkly-pigmented inner lining on the blind-side opercle in *S. melanurus*). *Symphurus civitatium* differs from the remaining four eastern Pacific species that have comparable meristic values in lacking a pupillary operculum (present in the others) and in having a fleshy ridge on the ocular-side lower jaw (absent in the others). *Symphurus civitatium* is further distinguished from *S. fasciolaris* and *S. melasmatotheca* in possessing 12 caudal fin rays (versus 10 and 11 in *S. fasciolaris* and *S. melasmatotheca*, respectively) and in lacking an ocellated spot on the caudal fin (present in *S. fasciolaris*) or pigmented peritoneum (present in *S. melasmatotheca*). *Symphurus civitatium* differs further from *S. atricaudus* and *S. williamsi* in lacking small ctenoid scales on the blind sides of the dorsal and anal fin rays (present in these other species). From *S. leei*, *S. civitatium* is further distinguished in having the head length considerably smaller than the body depth (versus head length nearly equal with body depth in *S. leei*), in having a smaller eye (13–21 SL vs. 22–27 SL in *S. leei*), and in having an unpigmented peritoneum (versus black in *S. leei*).

Material examined 298 specimens (22.0–149.0 mm SL).

Counted and measured (30 specimens, 48.8–149.0 mm SL). **Southeastern United States. North Carolina**: USNM 157403; Paratype (109); 35°21′10″, 75°22′40″; 26 m; 19 Oct 1884. **Florida**: TU 75907; 3(131–136); 27°35′04″N, 80°04′04″W; 26 m; 5 Sep 1965. UF 13062; (130); 28°35.5′N, 80°08′W; 62 m; 21 Feb 1965. USNM 154946; Paratype (139); Cape Canaveral; 18 m; 4 Apr 1940. **Gulf of Mexico. Alabama**: ALA 3015; 3(75.5–85.2); to 30 m; 1968. **Mississippi**: ALA 606.29; (94.4); Horn Island; Jul–Aug 1958. FMNH 45979; (110); 29°22′N, 88°40′W; 51 m; 22 Oct 1953. **Louisiana**: USNM 155227; Holotype (110); 29°06′30″N, 89°40′W; 17 m; 8 Jul 1938. USNM 313647; 2(48.8–72.2); Calcasieu Lake (ca. 30°N, 93°W); Feb 1982. **Texas**: FMNH 45109; 3(138–149); 27°43′N, 96°51′W; 27 m; 26 Sep 1950. USNM 313646; 9(88.6–108); 3 mi. offshore, Port Aransas (ca. 28°N, 97°W); 15 m; 16 Sep 1982. **Mexico**: IMS 544; 3(121–130); W Campeche; 27 m; 22–29 Jul 1951. UMML 34365; (130); 20°12′N, 91°40′W; 37 m; 11 Dec 1952.

Counted paratypes (148 specimens, 41 lots). **Gulf of Mexico. Florida**: USNM 86153; (120); St. Joseph's Bay; 27 Jan 1917. **Alabama**: USNM 157402; (117); Mobile; 13 m; 7 Feb 1917. **Louisiana**: USNM 86140; (120); Calcasieu Pass; 9 m; 15 Feb 1917. USNM 154945; 3(122–130); 28°54′N, 91°41.5′W; 18 m; 11 Jul 1938. USNM 154947; 5(110–123); 28°55.5′N, 91°46′W; 18 m; 11 Jul 1938. USNM 154948; 2(120–124); 28°58′N, 91°40.5′W; 16 m; 12 Nov 1938. USNM 154949; 2(105–129); 28°41.5′N, 91°10′W; 15 m; 11 Nov 1938. USNM 154950; 2(122–124); 28°47′N, 91°21.5′W; 11 Jul 1938. USNM 154951; (126); 29°12′N, 89°50.5′W; 13 m; 8 Jul 1938. USNM 154952; (117); 28°43′N, 91°13′W; 15 m; 11 Jul 1938. USNM 154953; 2(102–105); 29°12.5′N, 89°57′W; 7 m; 10 Jul 1938. USNM 154954; 3(114–118); 28°35.5′N, 91°01.5′W; 22 m; 13 Jul 1938. USNM 155226; (114); 28°45′N, 91°17.5′W; 16 m; 11 Jul 1938. USNM 157399; 3(109–121); Grand Terre; 2 Jul 1930. USNM 157400; 3(99.7–118); Grand Terre; 27 Jun 1930. **Texas**: USNM 86139; 2(118–126); Aransas Pass; 15 m; 5 Mar 1917. USNM 120081; (111); Galveston; 1941. USNM 120082; (81.5); Aransas Pass; 7 Aug 1941. USNM 157401; (117); Galveston; 10 m; 26–27 Feb 1917.

Counted (non-type material). Southeastern United States. Florida: UMML 34342; 3(136–140); 28°34′N, 80°15′W; 42 m; 19 Nov 1964. USNM 274484; (117); 28°13.5′N, 80°21′W; 22 m; 14 Nov 1963. USNM 291316; (132.0); 28°13′N, 80°21′W; 22 m; 14 Nov 1963. USNM 291317; 13(114–142); 28°13′N, 80°21′W; 22 m; 14 Nov 1963. UMML 34343; (131); 28°12′N, 80°05′W; 60 m; 14 Mar 1965. UMML 34344; (118); 27°57N, 80°03′W; 55 m; 28 Sep 1963. **Gulf of Mexico. Alabama**: ALA 301.17; 2(85.4–94.3); Dauphin Island; 28 Sep 1952. ALA 353.05; (108); Mobile Ship Channel; 6 Sep 1951. ALA 2385; 13(85.8–103); Dauphin Island; 15 Jul–20 Aug 1966. **Texas**: TCWC 4187.4; (100); 29°10′N, 94°30′W; 14 m; 28 Sep 1973. TCWC 4189.21; 18(97.8–124); 28°26′N, 95°23′W; 28 m; 29 Sep 1973. TCWC 4195.31; 9; 28°25N, 95°18′W; 35 m; 31 Oct 1973. UMML 34345; (128); 28°07′N, 95°53′W; 37 m; 26 Jan 1958. **Mexico**: FMNH 45427; 7(126–140); 20°18′N, 91°48′W; 42 m; 7 Dec 1952. UMML 34366; (130); 20°12′N, 91°40′W; 37 m; 11 Dec 1952. USNM 157693; 5(117–126); 20°05′N, 91°28′W; 31 m; 26 Aug 1951. USNM 157694; 3(128–132); 20°05′N, 91°28′W; 31 m; 26 Aug 1951. USNM 291318; (127); Campeche, Yucatan, 20°05′N, 91°28′W; 31 m; 26 Aug 1951. FMNH 46369; 11(115–138); 19°48′N, 91°20′W; 25 Aug 1951. GCRL 16383; 2(76.0–86.5); Lagunas de Terminos, Punta Zachtal, Campeche; 17 Nov 1970. IMS 543; 16(126–142); Pta Frontera; 31 m; 29 Jul–6 Aug 1951. USNM 274485; (132); N of Soto La Marina; 15 Mar 1947.

Other material examined (120 specimens, 22 lots). **Bermuda**: ANSP 137573; (79.3); washed onto shore. **Southeastern United States. North Carolina**: 3(22-24); Cape Fear River; Aug 1981; (uncatalogued reference specimens, CP&L Biol. Lab., Southport, NC 28461). **Florida**: UF 35486; (125); 29°58.1′N, 81°16.9′W; 14 m. TU 92501; 25(82.0–120); 29°11′05″N, 80°53′05″W; 12 m; 24 Feb 1970. UMML 34346; 3(118–134); 28°22′N, 80°05′W; 60 m; 14 Mar 1965. **Gulf of Mexico. Florida**: ANSP 94305; (25.0); Key West; 1 m; 21 Mar 1958. **Mississippi**: FMNH 45980; 2(110–120); 28°45′N, 89°15′W; 60 m; 23 Oct 1953. FMNH 86369; (113); 29°42′N, 88°29′W; 37 m; 10 Aug 1951. TU 5374; 18(113–137); 29°14.4′N, 88°52.4′W; 32 m; 11 Aug 1952. TCWC 2251.1; (126); 29°09′N, 88°52′W; 73 m; 10–16 Dec 1963. **Alabama**: FMNH 89568; 2(119–121); 29°42′N, 88°29′W; 37 m; 10 Aug 1951. ALA 798.14; 2(108–110); Gulf Shores, Breton Island; 3 Aug 1959. UF 70946; (115); 29°41′N, 88°14.5′W; 45 m; 22 Jul 1971. USA 1905; 25(91.9–122); 29°57′N, 87°54′W; 26 m; 20 Apr 1975. **Louisiana**: ANSP 55825; (125); Breton Island; Nov 1930. BMNH 1931.11.5:75; 1; Reversed Specimen; Breton Island. FMNH 45981; 2(109–119); 28°56′N, 89°09′W; 59 m; 25 Oct 1953. **Texas**: CAS-SU 40556; (133.4); Freeport; 28 Apr 1940. FMNH 79851; 3(139–152); 27°43′N, 96°53′W; 26 m; 14 Dec 1950. UMMZ 199071; 5(46.0–57.3); 8–9 Apr 1939. USA 4070; 20(111–127); 10 mi. SSE Port Aransas; 3 Dec 1975. **Mexico**: GCRL 16384; (32.7); Laguna el Carmen, Tabasco; 2 Mar 1978.

Symphurus tessellatus (Quoy and Gaimard 1824) Figures 2, 3, 4c, 6a

Synonymy

Plagusia tessellata Quoy and Gaimard 1824:240 (counts and color description; Rio de Janeiro Bay [= Guanabara Bay], Brazil).

Plagusia brasiliensis Agassiz, in Spix and Agassiz 1831:89 (counts, color description, and figure; Bahia, Brazil). Castelnau 1855:79 (brief description and figure). Whitehead and Myers 1971:495 (nomenclature and dating of Spix and Agassiz's Brazilian Fishes). Kottelat 1984:150 (listed in type catalogue of MHNN). Kottelat 1988:79 (nomenclature and type status of species described in Spix and Agassiz's Brazilian Fishes).

Aphoristia ornata. Kaup 1858:106 (in part) (synonymy; listed, South America). Günther 1862:490 (in part) (synonymized with *S. plagusia* Schneider, in Bloch and Schneider 1801; brief description; counts; Atlantic coasts of tropical America). Kner 1865-67: 292 (listed, Rio de Janeiro, Brazil).

Symphurus plagusia (not of Schneider, in Bloch and Schneider). Jordan and Goss 1889:324 (in part) (synonymy; in key; brief description; nomenclature; West Indies to Rio de Janeiro, Brazil). Jordan and Evermann 1898:2709 (in part) (after Jordan and Goss 1989). Berg 1895:79 (in part) (Mar del Plata–Montevideo; counts include those for *S. jenynsi*). Thompson 1916:416 (in part) (after Jordan and Goss; counts, measurements, brief color description). Devincenzi 1920:135 (Río de la Plata; distinguished from *S. jenynsi*). Devincenzi 1924–26:281 (listed, Uruguay; counts). Meek and Hildebrand 1928:1005 (in part) (color description; counts; Panama). Puyo 1949:178 (in part) (French Guyana; figure, counts, color description). Lowe-McConnell 1962:694 (in part) (listed, British Guiana). Caldwell 1966:84 (collections from offshore localities, Jamaica). Menezes and Benvegnú 1976:142 (synonymized with *S. plagusia*). Soares 1978:23 (listed, Rio Grande do Norte, Brazil; counts, color description, and figure). Lema et al. 1980:44 (Río de la Plata region, Rio Grande do Sul, Brazil; synonymy). Rosa 1980:222 (in part) (listed, nearshore and estuarine habitats, Paraiba, Brazil). Lucena and Lucena 1982:56 (listed, collections in southern Brazil). Matsuura *in* Aizawa et al. 1983:463 (listed, French Guiana and Surinam; counts, measurements, color photograph).

Aphoristia fasciata (not of DeKay). Goode and Bean 1896:458 (in key and figured; Jamaica).

Symphurus plagusia tessellata. Ginsburg 1951:199 (diagnosis and description of subspecies from Brazil-Uruguay). Ringuelet and Aramburu 1960:91 (in key; figure; synonymy; listed, Argentina). Carvalho et al. 1968:22 (in part) (synonymy; in key; brief description; occurrence in northern Brazil). Lazzaro 1973: 247 (in key; distribution in southern Brazil and Uruguay). Palacio 1974:87 (listed, north of Puerto, Colombia). Lazzaro 1977:70 (in key). Lema and Oliveira 1977:7 (recorded from Santa Catarina, Brazil; in key; suggested that *S. civitatium*, *S. tessellatus*, and *S. plagusia* are geographic races of the same species).

Symphurus plagusia plagusia (not of Schneider, in Bloch and Schneider). Cervigon 1966:816 (listed, Venezuela; probably *S. tessellatus* based on high meristic features, color description, and large sizes reported). Palacio 1974:87 (in part) (Colombia; specimens listed as *S. p. plagusia* were misidentified).

Symphurus pterospilotus (not of Ginsburg). Lema and Oliveira 1977:7 (in part) (specimens misidentified).

Diagnosis A *Symphurus* with the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal fin rays; unpigmented peritoneum; distinct, dark-brown or black, almost spherical blotch on the outer surface of the ocular-side opercle; 4–8 small ctenoid scales on the blind sides of the dorsal and anal fin rays (best developed on fin rays in posterior one-third of body in specimens >70 mm SL); lacking a fleshy ridge on the ocular-side lower jaw; 91–102 dorsal fin rays; 77–86, usually 78–84, anal fin rays; 49–54, usually 50–53, total vertebrae; 81–96, usually 83–93, scales in a longitudinal series; moderately long jaws usually extending to the vertical line through the middle or posterior margin of pupil of lower eye; moderately-sized eye (79–114 HL, $\bar{x}$ 95) without pupillary operculum; dorsal fin origin reaching the vertical line through the anterior margin of the upper eye, or occasionally only reaching the vertical through the middle of the upper eye; ocular surface dark- to light-brown, with 5–9 well-developed, sharply contrasting, relatively wide, dark-brown crossbands on head and trunk; inner lining of opercle and isthmus heavily pigmented on both sides of body; dorsal and anal fins without an alternating series of pigmented blotches and unpigmented areas; anterior dorsal and anal fin rays usually streaked with brown pigment; fin rays and membranes of dorsal and anal fins on posterior two-thirds of body becoming progressively darker posteriorly; males with posteriormost regions of fins almost uniformly black, while in females, posterior portions of fins, although darker than anterior regions, usually dark-brown and not as intensively pigmented as in mature males.

Description A large tonguefish, attaining adult sizes to 220 mm SL. ID pattern (Table 1) usually 1-4-3 (170/231 specimens), less frequently 1-5-3 (14), 1-4-2

Table 14

Summary of morphometrics expressed as thousandths of standard length (except SL in mm) for *Symphurus tessellatus* (*N* 22) and the possible holotype (MHNN 691) of *Plagusia brasiliensis* (a junior subjective synonym). (Abbreviations defined in Methods section.)

Character	Range	Mean	SD	*P. brasiliensis*
SL	97.9–203	145.0	27.66	140.3
BD	247–312	280.2	18.82	262
PDL	32–48	41.7	4.48	32
PAL	181–227	204.7	10.58	217
DBL	952–968	958.3	4.48	968
ABL	771–876	798.0	22.90	793
PL	44–73	59.0	6.47	43
PA	27–56	41.5	6.01	–
CFL	72–118	90.9	10.36	88
HL	170–199	186.6	7.37	175
HW	193–247	218.6	15.58	209
POL	117–135	125.9	5.38	117
SNL	35–46	40.3	2.55	32
UJL	41–52	46.3	3.12	41
ED	15–21	17.6	2.04	18
CD	33–63	46.4	6.51	36
UHL	113–163	143.3	12.03	120
LHL	80–114	97.8	10.56	94

Table 15

Summary of morphometrics expressed as thousandths of head length (except HL and HW) for *Symphurus tessellatus* (*N* 22) and the possible holotype (MHNN 691) of *Plagusia brasiliensis* (a junior subjective synonym). (Abbreviations defined in Methods section.)

Character	Range	Mean	SD	*P. brasiliensis*
HL/HW	1.1–1.4	1.2	0.08	1.2
POL	593–723	674.9	25.07	669
SNL	196–231	215.7	9.25	184
UJL	222–278	248.1	15.58	237
ED	79–114	95.2	10.06	106
CD	173–322	245.0	31.85	204
OPLL	243–359	306.8	31.68	–
OPUL	161–252	205.7	24.03	–
UHL	682–891	774.2	56.18	690
LHL	422–593	523.1	46.26	539

(10), or 1-3-3 (8). Caudal fin rays usually 12 (207/224), less frequently 10,11, or 13 (Table 2). Dorsal fin rays 91–102 (Table 3). Anal fin rays 77–86, usually 78–84 (Table 4). Total vertebrae 49–54, usually 50–53 (228/233) (Table 5). Hypurals 4. Longitudinal scale rows 81–96, usually 83–93 (Table 6). Scale rows on head posterior to lower orbit 18–23, usually 20–22 (Table 7). Transverse scales 38–45 (Table 8).

Proportional measurements appear in Tables 14 and 15. Body relatively elongate, only moderately deep (247–312 SL, $\bar{x}$ 280); greatest depth usually occurring in anterior third of body. Preanal length 181–227 SL, $\bar{x}$ 205. Head relatively short (170–199 SL, $\bar{x}$ 187); considerably shorter than body depth. Head relatively wide (193–247 SL, $\bar{x}$ 219), wider than head length (HW/HL 1.1–1.4, $\bar{x}$ 1.2); lower head lobe (80–114 SL, $\bar{x}$ 98) narrower in width than upper head lobe (113–163 SL, $\bar{x}$ 143). Lower opercular lobe on ocular side (243–359 HL, $\bar{x}$ 307) greater in width than upper opercular lobe (161–252, $\bar{x}$ 206). Postorbital length 117–135 SL, $\bar{x}$ 126. Snout (Fig. 4c) moderately long and somewhat pointed (196–231 HL, $\bar{x}$ 216); covered with small ctenoid scales. Anterior nostril, when depressed posteriorly, not reaching anterior margin of lower eye. Dermal papillae well developed on blind side of snout and chin regions, but not particularly dense, occasionally extending onto ocular-side snout. Jaws moderately long; upper-jaw length 222–278 HL, $\bar{x}$ 248; posterior extension of maxilla usually reaching to the vertical through the middle or posterior margin of pupil of lower eye. Ocular-side lower jaw lacking a fleshy ridge near posterior margin (Fig. 4c). Chin depth 173–322 HL, $\bar{x}$ 245. Lower eye moderate in size (79–114 HL, $\bar{x}$ 95); upper eye usually slightly anterior to lower eye; eyes not covered with scales; usually 1–3 small ctenoid scales in narrow interorbital space. Pupillary operculum absent. Length of dorsal fin base 952–968 SL, $\bar{x}$ 958. Dorsal fin origin (Fig. 4c) usually reaching to vertical line through anterior margin of upper eye, or occasionally only reaching vertical line through middle of upper eye; predorsal length 32–48 SL, $\bar{x}$ 42. Length of anal fin base 771–876 SL, $\bar{x}$ 798. Four to eight scales present on blind sides of dorsal and anal fin rays (best developed on fin rays in posterior third of body of specimens >70 mm SL). Pelvic fin length 44–73 SL, $\bar{x}$ 59; longest pelvic fin ray usually reaching base of first anal fin ray or occasionally falling short of that point; pelvic to anal fin distance 27–56 SL, $\bar{x}$ 42. Posteriormost pelvic fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly almost to origin of anal fin base (membrane torn in most specimens). Caudal fin relatively short, 72–118 SL, $\bar{x}$ 91.

Teeth well developed on blind-side jaws. Dentary on ocular side usually with single, mostly incomplete row of slender teeth; premaxilla on ocular side either with very short row of teeth anterior to vertical line equal with anterior nostril or lacking teeth altogether.

Scales large, strongly ctenoid on both sides of body.

Pigmentation General pattern of body pigmentation similar in both sexes at all sizes but usually more intense in sexually mature males. Males, especially those

in breeding condition (collected with gravid females), usually with more intense banding, dark-black fins, dark-black spot on ocular-side opercle, and, additionally, some specimens with irregularly-shaped, black pigment patches on posterior one-half of blind side of body. In contrast, mature females also with crossbands but less conspicuous than in males and with posterior portions of fins dark-brown but usually not black. Females lack black pigment patches on blind side observed in males.

Ocular-surface background pigmentation ranging from dark- to light-brown. Body usually with 5–9 (usually 5–7) well-developed, sharply contrasting, relatively wide, dark-brown crossbands on head and trunk. First two bands relatively consistent in position; first crossing head immediately posterior to eyes; second crossing body immediately behind opercular opening. Crossbands on trunk variable in number and degree of completeness, especially those between opercular opening and point about equal to two-thirds of trunk length. Males usually with 3–4 well-developed and lesser number of incomplete bands along trunk. Two posteriormost bands, just anterior to caudal fin base, slightly arched and usually darker than others on body. Blind side usually uniformly creamy-white; some mature males with irregular patches of black pigment on caudal one-third of blind side. Peritoneum unpigmented.

Outer surface of ocular-side opercle usually with distinct, dark-brown or black spot on ventral margin slightly forward of posterior margin of opercle. Opercular spot ranging from almost spherical to dorsoventrally-elongate black blotch covering most of lower opercle. Intensity of pigmentation in spot maximally developed in sexually mature adults. Inner linings of opercles and isthmus heavily pigmented on both sides of body. Pigment band well developed on ocular-side upper lip; ocular-side lower lip frequently spotted but without well-defined band.

Anterior dorsal and anal fin rays usually streaked with brown pigment, more heavily pigmented than connecting membranes. Fin rays and membranes of dorsal and anal fins on posterior two-thirds of body becoming increasingly darker posteriorly. Males with posteriormost regions of fins almost uniformly black, while in females, posterior portions of fins, although darker than anterior regions, usually dark-brown and not as intensively pigmented as in mature males.

Size and sexual maturity *Symphurus tessellatus* is one of the largest species in the genus and is the second largest Atlantic tonguefish species after *S. jenynsi* Evermann and Kendall (Ginsburg 1951, Menezes and Benvegnú 1976, Munroe 1987). Size-related life-history information is based on data from 385 fish. Males and females attain nearly similar sizes, but females are somewhat larger. The largest fish measured in this study was a female of 220 mm SL; the largest male measured 205 mm SL.

There were 214 males, 155 females, and 16 immature fish among material examined. There were 119 mature females ranging in size from 104 to 220 mm SL (Fig. 2). Based on reproductive stages for females, sexual maturity in this species occurs at sizes of 104–120 mm SL, but usually larger than 115 mm SL. Most mature females exceeded 140 mm SL, with only six smaller than 125 mm SL and two smaller than 110 mm SL present among fish examined. Twenty-six females of 49.5–119 mm SL were immature. The smallest of these, measuring 49.5 and 62.8 mm SL, had ovaries that were scarcely elongate. Other immature females, ranging from 68.6 to 119 mm SL, had only partially elongate ovaries with no indications of developing ova.

Geographic distribution (Fig. 3) A widespread tropical species, ranging in the north from the larger Caribbean Islands such as Cuba, Hispaniola, and Puerto Rico, southward to Uruguay. In the West Indies, adults and juveniles have frequently been taken in abundance at several localities, but the distribution of this species appears limited by the location of soft silt and mud sediments. These bottom types are more common on the larger islands that support river and estuarine habitats. The species has been taken at several inshore locations in Puerto Rico, Cuba, and Haiti, and a large number of adults were collected by the RV *Oregon* on the shelf area southwest of Jamaica (Caldwell 1966). Juveniles of this species have been taken from several inshore areas in Jamaica as well.

Along the continental margin it has been frequently captured on muddy bottoms from Belize and Nicaragua south to southern Brazil and Uruguay (ca. 37°S). In the northern part of its range along Central America, it has been collected as far north as Belize (17°12′N), but thus far is unknown from the Yucatan Peninsula or Campeche Bay. The absence of this species in the Yucatan region may be explained by upwelling (Rivas 1968) or by changes in the sediments of this region. The Yucatan Shelf is a broad limestone plateau with a minimum of land-derived detrital sediments (Harding 1964, Topp and Hoff 1972). Instead of soft silt and mud sediments typical of more southern locations, sediments on the inner shelf off the Yucatan Peninsula are firmer, consisting of skeletal remains of various planktonic and benthonic organisms, ooids, calcareous pellets, lithic fragments, and grapestone aggregates. This dramatic change from soft, mud substrates to firmer sediments in the Yucatan region may account for the absence of *S. tessellatus* in the waters off southern Mexico.

Symphurus tessellatus is one of the most abundant and frequently collected tonguefish species, especially in trawls, from Belize and Honduras south to Venezuela and along the entire coastline of northern South America from the Guianas to about southern Brazil (Meek and Hildebrand 1928, Cervigon 1966, Palacio 1974, Carvalho et al. 1968, Menezes and Benvegnú 1976). Menezes and Benvegnú (1976) described *S. tessellatus* as the most abundant tonguefish collected along the Brazilian coast from about 26°49′S to 4°S in northern Brazil. South of 28°S, it appears to be much rarer, and all specimens I examined from Rio Grande do Sul and south are juveniles. The small size of these specimens suggests that adult *S. tessellatus* may not be regular components of the ichthyofauna of Uruguay and northern Argentina, but that juvenile *S. tessellatus* either seasonally migrate, or are expatriated by passive transport, into waters along the continental shelf and coastline of Uruguay and northern Argentina. Thus it appears that the region south of Rio Grande do Sul, which comes under periodic influence from the cold Falkland Current, does not harbor large populations of this essentially tropical species so common in warmer waters further north.

The specimen from the inner continental shelf of Argentina described by Lazzaro (1973) as *S. plagiusa* and cited in the distribution section for *S. plagusia* (= *S. tessellatus* in the present study) by Menezes and Benvegnú (1976) is probably not a specimen of *S. tessellatus*. Based on the counts and figure provided by Lazzaro, it more closely matches meristic features and has the general body shape of *S. trewavasae*.

Bathymetric distribution Throughout its range, juvenile *S. tessellatus* are commonly taken by beach seine in nearshore habitats, and larger adults are frequently captured by trawl in deeper waters. Individuals have been collected from a depth range of 1–86 m (Table 11). There is an ontogenetic migration offshore. Juveniles occur commonly in medium- to high-salinity regions of estuaries and in high-salinity, soft-bottom habitats in nearshore mudflats. Adults generally range into deeper water, although a few large fishes I examined were taken in relatively shallow water. Most of the 349 *S. tessellatus* examined in this study were collected between 1 and 70 m (Table 11), but the majority of captures, and the center of abundance for this species, occurs in depths of 1–50 m (81% of the individuals in this study). The deepest captures are for a single specimen taken at 86 m and 21 individuals at 73 m. The majority of shallow-water captures were specimens smaller than 130 mm SL.

Interestingly, Menezes and Benvegnú (1976) reported that in southern Brazil, *S. tessellatus* (misidentified as *S. plagusia*) occurs only in shallow water (<12 m), though it is known to occur deeper in northern Brazil. They suggested that the presence of *S. jenynsi* off southern Brazil, which generally occurs on the continental shelf at depths greater than 12 m, somehow prevented the occurrence of *S. tessellatus* at these depths. Another explanation is that *S. tessellatus* is primarily a tropical species reaching its southern limit of distribution in southern Brazil south of Rio de Janeiro. Its bathymetric distribution in these waters may be limited not by competitive interaction from *S. jenynsi*; rather, the offshore distribution of *S. tessellatus* may be restricted by cooler water temperatures on the shelf. The appearance of *S. jenynsi*, a temperate-water species (Menezes and Benvegnú 1976), in these regions indicates that temperature may strongly influence the offshore distribution of *S. tessellatus* in southern Brazil.

Throughout its range to at least Rio de Janeiro, juvenile *S. tessellatus* occur in similar habitats and are often collected with a complete size range of *S. plagusia*. In the Caribbean, juvenile *S. tessellatus* are also taken with a complete size range of *S. caribbeanus*. Along the northeastern coast of South America from Surinam to eastern Brazil, large adults of this species are collected in deeper areas with a wide size range of specimens of *S. oculellus* and *S. diomedeanus*.

Remarks Comments regarding the nomenclatorial history of this species were reviewed under the "Remarks" section in the account of *S. plagusia*. All authors since Kaup (1858) have considered *S. tessellatus* and *S. plagusia* as conspecific. However, results of this study indicate that *S. plagusia* and *S. tessellatus* are both valid species.

The original description of *Plagusia tessellata* by Quoy and Gaimard (1824) provides sufficient information to clearly identify their specimen. This is the earliest name applied to a tonguefish collected from the southern Brazil region and, therefore, has priority over *Plagusia brasiliensis* Agassiz, in Spix and Agassiz 1831. *Plagusia brasiliensis* was collected at "Bahia," Brazil. The type specimen was thought to have been destroyed during the Second World War (Whitehead and Myers 1971). However, in two recent publications concerning authorship and existence of type specimens described in Spix and Agassiz's "Brazilian Fishes" (1829–31), Kottelat (1984) listed a specimen (MHNN 691) first as the holotype, and later (Kottelat 1988) as a possible syntype of *P. brasiliensis*, thus indicating the existence of at least one specimen from the original account of this nominal species. My examination of this specimen reveals that meristic features lie completely within the range of counts typical for *S. tessellatus* (ID pattern 1-4-3, caudal fin rays 12, dorsal fin rays 99, anal fin rays 83, total vertebrae 53, longitudinal scales 90,

scale rows on head 21, transverse scale count 42). Additionally, the specimen has small ctenoid scales on the blind sides of the dorsal and anal fin rays and a relatively large eye (10.6% HL), features characteristic of *S. tessellatus*. *Plagusia brasiliensis* is therefore regarded as a junior subjective synonym of *Symphurus tessellatus* (Quoy and Gaimard 1824).

In their revision of the tonguefishes occurring in the western South Atlantic, Menezes and Benvegnú (1976) reported that the species they identified as *S. plagusia* had high counts and that the pigmentation consisted of sharply contrasting crossbands with dorsal and anal fins becoming almost black in their posterior portions. These authors found little variation in their material and believed that only a single species was present on the inner continental shelf of southern South America. Menezes and Benvegnú (1976) used the oldest available name, *Symphurus plagusia* (Schneider, in Bloch and Schneider 1801), for their species. These authors also suggested that the subspecific designation for *S. plagusia*, as proposed by Ginsburg (1951), should be reexamined. Based on the high counts and color description of their specimens (strongly banded with fins becoming black posteriorly) and the capture location (open-shelf region where *S. plagusia* [*sensu strictu*] is rare), it is probable that Menezes and Benvegnú had studied only *S. tessellatus*.

Comparisons *Symphurus tessellatus* most closely resembles and is completely sympatric throughout the Caribbean and warmer waters of the western South Atlantic with *S. oculellus*, *S. caribbeanus*, and *S. plagusia*. *Symphurus tessellatus* differs from *S. oculellus* in having 4–8 small but well-developed scales on the blind sides of the dorsal and anal fin rays (especially evident in specimens >70 mm SL), a larger eye (79–114, $\bar{x}$ 95 HL in *S. tessellatus* vs. 68–104, $\bar{x}$ 84 HL), and lower meristic values (dorsal fin rays 91–102 vs. 99–106 in *S. oculellus*; anal fin rays 77–86 vs. 81–88; total vertebrae usually 50–53 versus 53–54). *Symphurus tessellatus* lacks a fleshy ridge on the ocular-side lower jaw that is usually present and well developed in *S. oculellus* (compare Figures 4c and 4d). Also, the posterior extension of the jaws is slightly less extensive in *S. tessellatus*, reaching only to about the vertical line through the rear margin of the pupil or rear margin of the lower eye. In *S. oculellus*, the jaws extend further backwards reaching a vertical line through the posterior margin of the eye, and in many specimens the jaws extend slightly posterior to the vertical line through the posterior margin of the lower eye.

Symphurus tessellatus generally has about nine wide, dark-brown crossbands; *S. oculellus* has 10–14 (usually 10–12) narrower crossbands. In *S. tessellatus* the caudal fin and the posterior one-third of the dorsal and anal fins are usually dark-brown or black and without an alternating series of blotches and unpigmented areas. In *S. oculellus*, the dorsal and anal fins are not uniformly dark-brown or black; instead, in the posterior two-thirds of the dorsal and anal fins there is an alternating series of blotches and unpigmented areas.

Symphurus tessellatus, especially juveniles and small adults (to ~150 mm SL), are superficially similar in overall body shape, relative eye size, and body pigmentation (crossbanding) to *S. caribbeanus*. However, *S. tessellatus* is easily distinguished from *S. caribbeanus* by the black spot on the outer surface of the ocular-side opercle and presence of scales on the blind sides of the dorsal and anal fin rays (both absent in *S. caribbeanus*), and *S. tessellatus* has the posterior dorsal and anal fins, as well as the caudal fin, uniformly darkly-pigmented without alternating blotches and unpigmented areas, and often has black pigment patches on the blind side of the body. In contrast, in *S. caribbeanus*, posterior regions of the vertical fins have alternating dark blotches and unpigmented areas without a progressive darkening in coloration posteriorly in these fins, and the blind side of the body lacks black pigment patches. *Symphurus tessellatus* also has modally higher counts than *S. caribbeanus* (total vertebrae 50–53 vs. 49–50 in *S. caribbeanus*; dorsal fin rays 91–102 vs. 89–96; anal fin rays 77–86 vs. 74–80; 81–96 scales in a longitudinal series vs. 78–89).

Symphurus tessellatus can readily be distinguished from *S. plagusia* and *S. civitatium*, and differences between these species were discussed in the "Comparisons" sections under the accounts for *S. plagusia* and *S. civitatium*, respectively.

Symphurus tessellatus is quite distinct from other Atlantic tonguefishes. Some meristic values of this species overlap those of *S. marginatus* (Goode and Bean) and *S. diomedeanus*, a species sometimes collected with *S. tessellatus*. Additionally, in the southern extent of its range *S. tessellatus* sometimes co-occurs with *S. jenynsi*.

Although *S. tessellatus* and *S. marginatus* have nearly complete overlap in fin-ray and vertebral counts, such similarities are the only ones between these otherwise distinctive species. Important differences between these species occur in ID pattern (1-4-3 vs. 1-3-2 in *S. marginatus*), hypural number (4 vs. 5), presence of scales on the blind sides of the dorsal and anal fin rays in *S. tessellatus* (absent in *S. marginatus*), and pigmentation features including an unpigmented peritoneum (black in *S. marginatus*), crossbanding on the body, and a black spot on the ocular-side opercle (vs. no crossbanding on body; instead, body with a dark blotch in the caudal region and no opercular spot in *S. marginatus*).

Despite co-occurrence and some morphological similarities, *S. tessellatus* is readily distinguished from *S. diomedeanus* and *S. jenynsi* in caudal-fin-ray number (12 in *S. tessellatus* vs. 10 in the others), and presence of scales on the blind sides of the dorsal and anal fin rays and presence of a black spot on the ocular-side opercle (absent in the others). *Symphurus tessellatus* differs further in lacking a pupillary operculum and the large pigmented spots in the dorsal and anal fins characteristic of *S. diomedeanus*. From *S. jenynsi*, *S. tessellatus* is further distinguished by its much lower meristic values, including 91–102 dorsal fin rays (vs. 107–115), 77–86 anal fin rays (vs. 91–99), and 49–54 total vertebrae (vs. 57–60 in *S. jenynsi*).

There are nine eastern Pacific *Symphurus* with somewhat similar ID patterns, comparable fin-ray counts, or pigment patterns reminiscent of those observed in *S. tessellatus*. Of these nine, only *S. chabanaudi* Mahadeva and Munroe and *S. elongatus* (Günther) are similar to *S. tessellatus* in that they lack a pupillary operculum. Of all species in the genus, *S. tessellatus* is most similar in form, size, and pigmentation pattern to *S. chabanaudi*. However, *S. tessellatus* is distinguished from *S. chabanaudi* primarily by modal differences in the number of dorsal (91–102 vs. 98–109 in *S. chabanaudi*) and anal fin rays (74–86 vs. 82–92); total vertebrae (48–54, usually 50–53 vs. 52–57, usually 53–56); and scales in a longitudinal series (81–96 vs. 92–102 in *S. chabanaudi*). The two species also differ in relative frequencies of occurrence of particular ID patterns. In *S. chabanaudi*, 50% (49/95) of the individuals had a 1-5-3 ID pattern while only 30% (28 specimens) featured a 1-4-3 pattern. In contrast, 173 of 233 (74%) *S. tessellatus* possessed a 1-4-3 ID pattern, while only 6% (13 specimens) had a 1-5-3 pattern.

There is some overlap in fin-ray and vertebral counts between *S. tessellatus* and *S. elongatus*; however, these overlaps are the only similarities between these otherwise distinctive species. *Symphurus tessellatus* has a pattern of crossbands on the body and a large black blotch on the ocular-side opercle, whereas in *S. elongatus* the body is uniformly pigmented without crossbands and this species lacks the prominent black blotch on the ocular-side opercle. Further differences include the presence of small ctenoid scales on blind sides of the dorsal and anal fin rays in *S. tessellatus* (absent in *S. elongatus*) and absence of a fleshy ridge on the ocular-side lower jaw in *S. tessellatus* (a well-developed ridge present in *S. elongatus*). *Symphurus tessellatus* also has a much larger eye (15–21 SL) compared with that of *S. elongatus* (9–15 SL).

The remaining seven eastern Pacific species with meristics comparable to those observed in *S. tessellatus* include *S. fasciolaris*, *S. leei*, *S. atricaudus*, *S. melanurus*, *S. williamsi*, *S. melasmatotheca*, and *S. undecimplerus* Munroe and Nizinski. As mentioned above, all of these species, in contrast to *S. tessellatus*, possess a pupillary operculum, and none have the black spot on the ocular-side opercle characteristic of *S. tessellatus*. *Symphurus tessellatus* differs further in caudal-fin-ray number (12) from *S. fasciolaris* (10) and *S. melasmatotheca* and *S. undecimplerus* (each with 11 caudal fin rays). *Symphurus tessellatus* is distinguished from *S. melanurus* in lacking a fleshy ridge on the ocular-side lower jaw (present in *S. melanurus*), in having small ctenoid scales on the blind sides of the dorsal and anal fin rays (usually none or occasionally 1–3 small scales at bases of fin rays in *S. melanurus*), and in having the first dorsal fin ray placed posterior to a vertical through the front margin of the upper eye (versus first dorsal fin ray placed anteriorly to a vertical through front margin of upper eye in *S. melanurus*). *Symphurus tessellatus* is further distinguished from *S. williamsi* in having crossbanding on the body with the posterior portions of the dorsal and anal fins considerably darker than the anterior portions (versus uniform body color without prominent crossbanding and no posterior darkening of dorsal and anal fins in *S. williamsi*). *Symphurus tessellatus* differs from *S. leei* in having an unpigmented peritoneum (versus black in *S. leei*), and the length of the head is smaller than the body depth in *S. tessellatus* (nearly equal to body depth in *S. leei*). *Symphurus tessellatus* is further distinguished from *S. atricaudus* in that it lacks the small ctenoid scales on the ocular-side dorsal and anal fin rays characteristic of that species.

Material examined 454 specimens (13.4–220 mm SL).

Counted and measured (23 specimens, 96.6–203 mm SL). **Puerto Rico**: UPRM 2717; (142); Puerto Rico; 8 m; 14 Mar 1966. UPRM 2760; (142); Mayaguez; 12 m; 15 Mar 1966. UPRM 2859; (111); Mayaguez; 9 m; 29 Apr 1966. UPRM 3758; (130); Anasco River; 1–2 Jul 1953. UPRM 3759; 2 (130–133); Mayaguez Bay; 1966. **French Guiana**: UF 35275; (172); 5°14′N, 52°06′W; 45 m; 11 Dec 1977. **Brazil**: UFPB 143; 5(96.6–135); Rio Paraiba do Norte; 27 Apr 1978. MHNN 691; (140.3); Bahia (possible holotype or syntype of *Plagusia brasiliensis*). ANSP 121549; 10(108–203); Rio de Janeiro; Jul–Aug 1963.

Counted (234 specimens, 64 lots). **Puerto Rico**: MCZ 28843; (91.8); Puerto Rico; 1898–99. UF 83996; (146); beach at Mani, just N of Mayaguez; 16 Apr 1964. UPRM 1590; 2(159–173); Mayaguez; 3 Mar 1962. UPRM 2743; 15(114–172); Mayaguez; 6 m; 15 Mar 1966. UPRM 3760; 2(128–143); Rio Anasco; 17 Aug 1951. UPRM 3761; 3(126–158); Mayaguez Bay; 1966. USNM 126448; (132); Mayaguez; 1899. **Cuba**: MCZ 11269; (111); Cuba. USNM 35108; (81.3); Havana. USNM 37750; (68.6); Havana. USNM 154857; (131); Cuba. **Dominican Republic**: USNM 108369; (123). USNM 108372; (126). **Haiti**: ANSP 81861; (97.7); Port-au-Prince; Nov 1949. ANSP 83626; 8(83.3–113); Port-au-Prince; 1949. ANSP 97661; 6(114–146); Port-au-Prince; 1936. UMMZ 142422; (127); Haiti; 15 Apr 1983. USNM 133671; 3(109–124); Port-au-Prince; 1–4 Jan 1947. USNM 164849; 2(87.7–133); Haiti; 1927. **Jamaica**: LACM 6215; (142); 17°52′N, 77°53′W; 40 m; 15 May 1962. LACM 6217; 10(123–

152); 17°46′N, 77°30′W; 16 m; 15 May 1962. UMML 4831; (115); Hunts Bay; 3 Aug 1958. UMML 34367; 3(118–160); 17°45′N, 77°38′W; 35 m; 15 May 1962. UMML 34368; (144); 17°55′N, 77°51′W; 39 m; 18 May 1965. USNM 37348; (79.9); Jamaica. USNM 291333; 6(128–161); 17°55′N, 77°51′W; 40 m; 18 May 1965. USNM 291347; 2(130–146); 17°53′N, 77°50′W; 42 m; 18 May 1965. USNM 291346; 2(128–138); 17°51′N, 77°49.5′W; 49 m; 18 May 1965. **Belize**: UMML 34354; 4(132–160); 17°12′N, 88°11.2′W; 19 m; 9 May 1967. UMML 34355; 9(134–160); 17°12′N, 88°11.2′W; 19 m; 18 May 1967. **Honduras**: FMNH 100384; 5(38.1–56.0); Brus Lagoon; 10 May 1975. FMNH 94819; 5(37.7–49.5); Brus Lagoon; 10 May 1975. UMML 34348; 2(130–134); 15°49.15′N, 83°44′W; 31 m; 7 Apr 1967. UMML 34349; 2(126–141); 15°48′N, 83°54′W; 24 m; 7 Apr 1967. UMML 34350; 5(111–164); 15°49.5′N, 83°44′W; 31 m; 7 Apr 1967. UMML 34351; 3(130–148); 15°54′N, 83°40′W; 37 m; 8 Apr 1967. UMML 34352; 3(132–155); 15°54′N, 83°40′W; 37 m; 8 Apr 1967. UMML 34353; 2(138–147); 15°45′N, 83°32′W; 35 m; 9 Apr 1967. **Panama**: GCRL 12698; 2(13.4–65.8); Canal Zone; 5 Mar 1974. FMNH 18251-57; 7(50.3–73.3); Panama. **Colombia**: UMML 34369; 4(145–155); 10°53′N, 75°22′W; 42 m; 23 May 1964. UMML 34356; (148); 9°30′N, 76°07.5′W; 41 m; 26 May 1964. USNM 291332; (147); 8°59′N, 76°27′W; 26 m; 29 Nov 1968. **Venezuela**: ANSP 121394; 7(67.9–152); Venezuela; 15 Mar 1962. FMNH 88650; 16(155–200); 12°19′N, 70°34′W; 73 m; 27 Sep 1963. UMML 34370; (173); 11° 52′N, 70°22′W; 35 m; 27 Jun 1968. UMML 34357; (171); 12°19′N, 70°34′W; 73 m; 27 Sep 1963. UMML 34358; (145); 10°29′N, 62° 30′W; 9 m; 24 Oct 1963. **Trinidad**: UPRM 3762; (142); Trinidad; 4 May 1964. **Guyana**: FMNH 86364; (162); 8°09′N, 58°23′W; 42 m; 29 Aug 1958. FMNH 90546; 23(152–204); 8°32′N, 59°10′W; 43 m; 28 Oct 1958. GCRL 3835; (196); 8°13′N, 58°40′W; 37 m; 27 Apr 1969. GCRL 3838; 3(192–202); 9°14′N, 60°19′W; 44 m; 25 Apr 1969. **Surinam**: FMNH 86459; (161); Surinam; *Coquette* 1957. GCRL 23512; 6(164–196); 6°56′N, 54°05′W; 59 m; 2 May 1969. USNM 291335; (168); 6°12′N, 53°23′W; 46 m; 1 Jul 1972. **Brazil**: FMNH 90544; 3(183–196); 1°57′N, 48°12′W; 55 m; 14 Nov 1957. FMNH 91129; (197); 2°29′N, 48°54′W; 86 m; 15 Nov 1957. MCZ 11381; 14(93.9–202); Rio de Janeiro; 1865. MCZ 24939; (174); Rio de Janeiro; 1865. UFPB 1120; 5(51.5–115); Rio Paraiba do Norte; 30 Aug 1981. UFPB uncat.; 9(55.7–123); Rio Paraiba do Norte; 13 Nov 1981. UFPB uncat.; 2(100–110); Rio Paraiba do Norte; 30 Jul 1981. USNM 159225; 2(182–187); 1°57′N, 48°12′W; 55 m; 17 Nov 1957.

Other material examined (197 specimens, 70 lots). **Cuba**: MCZ 91961; (89.9); Cuba. **Honduras**: UF 33892; 4(138–154); 15°45′N, 83°32′W; 35 m; 9 Apr 1967. USNM 291345; 6(136–161); 15°56′N, 83°55′W; 47 m; 2 Feb 1967. **Nicaragua**: UMML 34359; 2(126–140); 11°51′N, 83°35′W; 20 m; 28 Jan 1971. UMML 34360; 9(56.4–142); 12°16′N, 83°31′W; 12 m; 28 Jan 1971. **Panama**: GCRL 14930; 2(173–177); Colon; Apr 1974. MCZ 58656; (31.1); Panama; 9 Sep 1964. UF 75622; (57.5); Canal Zone; 1974. UF 76003; (62.8); Canal Zone; Aug 1974. UMML 26664; 2(123–141); 9°18.2–18.4′N, 80°03.3–04′W; 24 m; 20 Jul 1966. USNM 81652; (89.4); Porto Bello; 24–28 Apr 1911. USNM 81653; 2(61.1–67.6); Fox Bay; 11 Jan 1911. USNM 81655; 2(38.1–43.5); Fox Bay; 27 Jan 1912. USNM 144792; (65.1); Canal Zone; 4 Mar 1937. USNM 291351; 3(170–208); 8°25′N, 79°56′W; 10 m; 19 Dec 1963. USNM 291354; 5(189–220); 8°25′N, 79°56′W; 10 m; 19 Dec 1963. **Colombia**: UMML 22247; 22(84–148); 8°48–46.8′N, 76°39.7–42.8′W; 20 m; 12 Jul 1966. UMML 31320; (133); 8°51.9–53.9′N, 76°37.2′W; 12 Jul 1966. USNM 291350; (152); 8°50′N, 76°48′W; 49 m; 2 Nov 1970. USNM 291353; (194); 6°46′N, 54°27′W; 49 m; 28 Jun 1972. USNM 291356; 9(191–207); 6°54′N, 53°58′W; 64 m; 30 Jun 1972. USNM 291352; 3(162–173); 6°34′N, 54°28′W; 37 m; 28 Jun 1972. **Venezuela**: ANSP 120209; (133); Venezuela; 23 Jul 1960–17 Mar 1962. GCRL 3837; (163); 8°52′N, 59°58′W; 29 m; 26 Apr 1969. MCZ 41081; (104); 10°17′N, 69°45′W; 1958. UMML 30197; 30(84–183); 11°25.1–25.8′N, 70°52.1–50′W; 18 m; 27 Jul 1968. UMML 30223; (160); 11°55–55.3′ N, 70°59.9′–71°00′W; 11 m; 28 Jul 1968. UMML 34361; 2(138–185); 10°49′N, 63°13′W; 48 m; 19 Jul 1968. UMML 34362; (187); 10°36′N, 68°12′W; 24 m; 25 Jul 1968. UMML 34363; 6(158–201); 10°11′N, 64°48′W; 35 m; 19 Oct 1963. USNM 291355; 10(144–197); 12°17′N, 70°34′W; 73 m; 27 Sep 1963. USNM 291348; 4(161–185); 11°50′N, 70°40′W; 59 m; 10 May 1965. **Trinidad**: USNM 113251; (124); 10°37′N, 61°42′W; 60 m; 3 Feb 1884. USNM 123112; (179); Gulf of Paria. **French Guiana**: UF 44365; (168); 5°05′N, 51°58′W; 45 m; 11 Dec 1977. **Surinam**: UMML 12251; (162); 6°18′N, 55°11′W; 18 m; 20 Feb 1963. USNM 159536; (177); 6°41′N, 54°17′W; 46 m; 14 Jun 1957. USNM 159567; (205); 6°42′N, 54°12.5′W; 44 m; 14 Jun 1951. USNM 159612; (204); 6°41.5′N, 54°14.5′W; 44 m; 14 Jun 1957. USNM 159618; (194); 6°42.5′N, 54°10′W; 42 m; 14 Jun 1957. USNM 291349; (82.3); 5°30′N, 52°10′W; 51 m; 12 Sep 1958. USNM 291358; 5(126–142); 9°33′N, 76°02′W; 49 m; 28 Nov 1968. **Brazil**: USNM 159237; 6(165–191); 2°00′N, 48°19′W; 46 m; 16 Nov 1957. FMNH 88193; (160); Bahia; 13 Apr 1908. MCP 1198; (116); Florianopolis; 30 Oct 1968. MCP 1199; (114); Florianopolis; 30 Oct 1968. MCP 1200; (118); Florianopolis; 30 Oct 1968. MCP 1202; (116); Florianopolis; 30 Oct 1968. MCP 2193; (156); Florianopolis; Oct 1968. MCP 2194; (112); Florianopolis; Oct 1968. MCP 3139; (126); Florianopolis; Oct 1968. MCP 5663; (180); Port Belo, Santa Catarina. MCP 7270; (128); Port Belo, Santa Catarina; 3–4 Nov 1973. MCP 7327; (126); Porto Belo, Santa Catarina; 1 Aug 1973. MCP 7345; (130); Porto Belo, Santa Catarina; 31 Jul–1 Aug 1973. MCZ 889; 2(123–139); Rio de Janeiro. MCZ 11149; (160); Rio de Janeiro. MCZ 11323; (105); Pernambuco. MCZ 11378; 3(68.7–96.1); Pernambuco. MCZ 11379; (147); Santos. MCZ 11380; (91.7); Curuca. MCZ 11382; (137); Rio de Janeiro. UF 19938; 3(109–133); Sao Paulo; 13 Jul 1961. UFPB 882; 5(36.0–115); Cabedelo; 29 Oct 1981. UFPB uncat.; 5(57.8–107); Ilha da Restinga, Rio Paraiba do Norte. UMML 13292; (186); 4°38′N, 51°05′W; 59 m; 26 Feb 1963. UMML 13977; (157); 2°10′S, 42°24′W; 48 m; 11 Mar 1963. USNM 83172; (94.4); Rio de Janeiro. **Uruguay**: USNM 87772; (119); Montevideo. USNM 87773; (113); Montevideo.

Symphurus oculellus, new species
Figures 2, 4d, 5, 6b–c

Synonymy

Symphurus atricaudus (not of Jordan and Gilbert 1880). Puyo 1949:179 (French Guyana; counts, color description, poor figure; distinguished from *S. plagusia*).

Diagnosis A *Symphurus* characterized by the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal fin rays; unpigmented peritoneum; lacking small ctenoid scales on the blind sides of the dorsal and anal fin rays; prominent fleshy ridge on ocular-side lower jaw; no pupillary operculum; 99–106 dorsal fin rays; 81–88, usually 83–88, anal fin rays; 52–55, usually 53–54, total vertebrae; 85–98, usually 86–93, scales in longitudinal series; relatively long jaws with posterior extension of maxilla usually reaching to the vertical through posterior margin of pupil of lower eye, occasionally extending to or slightly beyond the vertical through posterior margin of lower eye; relatively small eye (68–104 HL, $\bar{x}$ 84); dorsal fin origin usually at or occasionally slightly anterior to the vertical line through the anterior margin of upper eye; ocular surface dark- to light-brown with 10–14 well-developed, sharply contrasting, somewhat narrow, dark-brown crossbands on head and trunk; outer surface of ocular-side opercle with dark melanophores in diffuse circular pattern or with melanophores coalesced into somewhat rounded pigment spot; inner lining of opercle and isthmus more heavily pigmented on ocular surface than blind side; and dorsal, anal, and caudal fins with an alternating series of pigmented blotches and unpigmented areas.

Table 16
Summary of morphometrics expressed in thousandths of standard length (except SL in mm) for the holotype (USNM 159606) and 13 paratypes of *Symphurus oculellus*. (Abbreviations defined in Methods section.)

	Holotype	Paratypes			
Character	(USNM 159606)	*N*	Range	Mean	SD
SL	144.1	14	75.8–164	142.5	21.09
BD	271	14	231–297	274.5	17.19
PDL	32	13	32–47	38.6	4.13
PAL	199	14	189–243	205.6	13.32
DBL	968	13	953–968	961.4	4.13
ABL	795	14	765–837	793.7	18.74
PL	53	12	40–64	54.3	6.08
PA	37	12	20–60	41.2	12.62
CFL	90	14	80–99	88.9	5.53
HL	180	14	168–218	182.3	11.58
HW	209	14	198–281	216.8	21.37
POL	126	14	112–153	124.8	9.38
SNL	37	14	34–46	38.0	3.21
UJL	46	14	37–50	43.3	3.24
ED	12	14	12–19	15.4	1.95
CD	50	14	39–63	45.4	6.39
UHL	140	14	126–151	139.4	6.81
LHL	98	14	79–111	92.9	8.13

Description *Symphurus oculellus* is a relatively large tonguefish attaining maximum lengths of approximately 189 mm SL. ID pattern usually 1-4-3 (33/38), infrequently 1-3-4 (2), 1-5-3 (1), 1-4-2 (1), or 1-3-3 (1) (Table 1). Caudal fin rays 12 (49/53 specimens), less frequently 11 (Table 2). Dorsal fin rays 99–106 (Table 3). Anal fin rays 81–88, usually 83–88 (Table 4). Total vertebrae 52–55, usually 53–54 (34/37) (Table 5); abdominal vertebrae 3+6. Hypurals 4. Longitudinal scale rows 85–98, usually 86–93 (Table 6). Scale rows on head posterior to lower orbit 19–23, usually 19–20 (Table 7). Transverse scales 36–42, usually 38–40 (Table 8).

Proportional measurements appear in Tables 16 and 17. Body relatively elongate with gradual taper posteriorly; body depth relatively narrow (231–297 SL, $\bar{x}$ 274), and nearly uniform from vertical through anal fin rays 10–15 and extending posteriorly to mid-point of body. Preanal length 189–243 SL, $\bar{x}$ 206; somewhat shorter than body depth. Head relatively short (168–218 SL, $\bar{x}$ 182), shorter than body depth. Head relatively wide (198–281 SL, $\bar{x}$ 217); usually greater than head length (HW/HL 1.1–1.5, $\bar{x}$ 1.2); lower head lobe (79–111 SL, $\bar{x}$ 93) considerably narrower than upper head lobe (126–151 SL, $\bar{x}$ 139). Lower opercular lobe of ocular side (264–341 HL, $\bar{x}$ 292) wider than upper opercular lobe (174–246 HL, $\bar{x}$ 211). Postorbital length 112–153 SL, $\bar{x}$ 125. Snout (Fig. 4d) moderately long (190–227 HL, $\bar{x}$ 209), slightly rounded or truncate, covered with small ctenoid scales. Anterior nostril not reaching anterior margin of lower eye when depressed posteriorly. Dermal papillae well developed on blind-side snout and chin regions, but not particularly dense, occasionally extending onto ocular-side snout. Jaws relatively long; upper jaw length 221–258 HL, $\bar{x}$ 238; posterior extension of maxilla usually reaching to vertical through posterior margin of pupil of lower eye, occasionally to or slightly beyond vertical through posterior margin of lower eye. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin (Fig. 4d). Chin depth 214–291 HL, $\bar{x}$ 248. Lower eye relatively small (68–104 HL, $\bar{x}$ 84); upper eye usually slightly anterior to lower eye; eyes not covered with scales; usually only 1–3 small, ctenoid scales in narrow interorbital space. Interorbital space sometimes equaling half the diameter of the lower eye. Pupillary operculum absent. Length of dorsal fin base 953–968 SL, $\bar{x}$ 961. Dorsal fin origin (Fig. 4d) usually at, or occasionally slightly anterior to, vertical line through an-

Table 17
Summary of morphometrics expressed as thousandths of head length (except HW/HL) for the holotype (USNM 159606) and 13 paratypes of *Symphurus oculellus*. (Abbreviations defined in Methods section.)

	Holotype	Paratypes		
Character	(USNM 159606)	Range	Mean	SD
HW/HL	1.2	1.08–1.53	1.2	0.11
POL	700	651–722	683.8	20.64
SNL	204	190–227	209.0	11.67
UJL	254	221–258	238.3	11.74
ED	69	68–104	84.3	10.52
CD	277	214–291	248.4	23.62
OPLL	308	264–341	292.3	23.77
OPUL	200	174–246	210.6	20.39
UHL	777	661–814	767.4	44.73
LHL	542	464–556	510.3	28.01

terior margin of upper eye; predorsal length 32–47 SL, $\bar{x}$ 39. Length of anal fin base 765–837 SL, $\bar{x}$ 794. Scales absent from distal two-thirds of blind-side dorsal and anal fin rays. Occasionally with one or two scales occurring sporadically on some blind-side dorsal and anal fin-ray bases. Pelvic fin relatively short, 40–64 SL, $\bar{x}$ 54; longest pelvic fin ray extending posteriorly to base of first or occasionally second anal fin ray; pelvic to anal fin distance 20–60 SL, $\bar{x}$ 41. Posteriormost pelvic fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly to origin of anal fin base (membrane torn in most specimens). Caudal fin relatively short, 80–99 SL, $\bar{x}$ 89.

Teeth well developed on blind-side jaws. Dentary on ocular side usually with single, mostly incomplete row of slender teeth; premaxilla on ocular side either lacking teeth altogether, or with very short row of teeth covering no more than one-third of premaxilla anterior to the vertical equal with the anterior nostril.

Scales large, ctenoid on both sides of body.

Pigmentation Ocular surface ranging from dark- to light-brown with 10–14 (usually 10–12) well-developed, sharply contrasting, somewhat narrow, dark-brown crossbands on head and trunk. Anteriormost crossband on head immediately posterior to eyes; second band situated short distance (usually only 3–4 scales) posteriorly. Throughout most of their vertical extent, two anteriormost bands separate; several specimens with first two crossbands coalesced on ventral portion of opercle forming wide, somewhat circular spot. Crossbands on head somewhat narrower than those on mid- and posterior portions of body. Number of crossbands on trunk variable, differing in degree of completeness, especially in region between opercular opening to point about two-thirds of trunk length. Some bands on body complete, continuous on dorsal and anal fins as dark-brown blotches. Posteriormost crossband situated short distance from caudal fin base, somewhat expanded and slightly arched. Blind side creamy-white. Peritoneum unpigmented. Membrane on blind-side ovary with diffuse pattern of small melanophores (visible only by dissection).

Outer surface of ocular-side opercle with dark melanophores in diffuse pattern or with melanophores sometimes coalesced into somewhat rounded pigment spot. Inner lining of opercle and isthmus more heavily pigmented on ocular surface; blind-side inner opercle with pigmentation restricted to small band of pepper-dot melanophores along ventral margin. Isthmus on blind side not heavily pigmented, but often with pepper-dot pattern of melanophores. Pigment band well developed on ocular-side upper lip; ocular-side lower lip frequently spotted but without well-defined pigment band.

Dorsal, anal, and caudal fins with alternating series of blotches and unpigmented areas. Dorsal fin scarcely pigmented in anterior one-half of body; with series of alternating blotches and unpigmented areas beginning at approximately body mid-point and continuing to posteriormost extent of fin. Anterior one-fourth of anal fin without blotches; posterior three-fourths with pattern of alternating blotches and unpigmented areas as in dorsal fin. Blotches on dorsal and anal fins 3–5 fin rays wide including adjoining membrane. Both dorsal and anal fins with blotches coalescing in posterior one-sixth of fins and forming continuous pigmentation band on fins. Posterior portions of fins becoming gradually darker; blotches, although still present, much more difficult to discern. Distal two-thirds of caudal fin heavily pigmented; proximal one-third relatively lightly pigmented. Caudal fin of most specimens not uniformly pigmented; small cluster of rays (usually 2–4) more lightly pigmented giving appearance of alternating darkly- and lightly-pigmented areas. Smaller number of specimens with entire caudal fin heavily pigmented without pattern of alternating dark and light pigmentation.

Size and sexual maturity Among material examined, there were 39 males, 23 females, and five specimens of unknown sex. No significant differences were found between the sexes in overall size; males ranged from 82.2 to 189 mm SL, females were 75.8–180 mm SL. Based on reproductive stages of females, this species attains sexual maturity at about 110 mm SL (Fig. 2). All females larger than 111 mm SL had elongate ovaries. The smallest female, an immature fish of 75.8 mm SL, had only partially elongate ovaries. The

next smallest female was 111 mm SL and had small developing ova in the gonads. All other females were larger than 130 mm SL, had elongate ovaries, and were considered sexually mature.

Etymology From the latin "oculus" (eye), plus "ellus" (little), in reference to the relatively small size of the eye in this species compared with that of *S. tessellatus*.

Geographic distribution (Fig. 5) A tropical species with a fairly restricted distribution along the inner continental shelf of northeastern South America from Guyana (57°W) to northeastern Brazil (2°S, 40°W) where the majority of specimens have been collected. All but one specimen (UMML 12265; 2°20'S) were collected north of the Amazon outflow. Since little systematic sampling has been conducted on the inner continental shelf off equatorial Brazil, it is not known whether the new species occurs more frequently in areas immediately south of the outflow from the Amazon River.

Bathymetric distribution *Symphurus oculellus* occurs at moderate shelf depths (7–110 m) and does not appear to utilize nearshore habitats or estuarine environments as nursery areas as do *S. plagusia* and *S. tessellatus*. Specimens ranging from 76 to 189 mm SL have been collected in offshore habitats, with most (52/57, or 91%) being collected between 11 and 70 m (Table 10). At these depths, it is occasionally collected with adult *S. tessellatus*; however, size differences between the two species in these collections are quite striking. All *S. tessellatus* collected with *S. oculellus* were large adults (>130 mm SL), while the *S. oculellus* were a mixture of sizes, with juveniles as small as 78 and 82 mm SL.

Remarks Not all specimens that are the basis of citations in the synonymies of *S. plagusia* and *S. tessellatus* could be examined, so it is impossible to determine if any specimens of *S. oculellus* were included among material listed in earlier accounts on *Symphurus* from northern South America. It is possible that specimens of *S. oculellus* were included in the study by Lowe-McConnell (1962), since some of the trawl stations in that study were at appropriate depths to capture *S. oculellus*. Lowe-McConnell listed all tonguefish captured as *S. plagusia* but did not include descriptive accounts for the specimens, thus preventing positive identification.

The fish described by Puyo as *S. atricaudus* (Jordan and Gilbert) is clearly *S. oculellus*. *Symphurus oculellus* may be distinguished from the eastern Pacific *S. atricaudus* by the following characters: dorsal fin rays 99–106 vs. 94–101 in *S. atricaudus*; anal fin rays 81–88 vs. 77–84; scales 85–98 vs. 104–115. Additionally, *S. oculellus* lacks a pupillary operculum and scales on the blind-side posterior rays of the dorsal and anal fins (both present in *S. atricaudus*).

Comparisons Among Atlantic members of the *S. plagusia* complex, *S. oculellus* most closely resembles and is largely sympatric with *S. tessellatus* and *S. plagusia*. Characteristics distinguishing *S. oculellus* from these species were discussed in the "Comparisons" sections under the accounts for *S. plagusia* and *S. tessellatus*, respectively. *Symphurus oculellus* is most easily distinguished from the two remaining Atlantic species belonging to this complex (*S. civitatium* and *S. caribbeanus*) by differences in counts for dorsal fin rays (99–106 vs. 96 or fewer in *S. caribbeanus* and *S. civitatium*), anal fin rays (81–89 vs. 80 or fewer), and total vertebrae (52–55 versus 51 or fewer in *S. caribbeanus* and *S. civitatium*).

Among other Atlantic *Symphurus*, some meristic values of *S. oculellus* overlap those of three relatively deep-water species: the eastern Atlantic *S. vanmelleae* Chabanaud and *S. ligulatus* Cocco, and the western Atlantic *S. marginatus*. Additionally, *S. oculellus* has pigmented dorsal and anal fins reminiscent of those of the sympatrically occurring *S. diomedeanus*. Comparable fin-ray or vertebral counts are the only similarities between *S. oculellus* and the deep-water species. *Symphurus oculellus* is otherwise distinctive from all three species in ID pattern (1-4-3-2-2 vs. 1-2-2-1-2 in *S. vanmelleae*, 1-2-2-2-2 in *S. ligulatus*, and 1-3-2-2-2 in *S. marginatus*), peritoneal pigmentation (unpigmented versus black in the others), and pigmentation of the dorsal and anal fins (alternating series of blotches and unpigmented areas in *S. oculellus* versus uniformly pigmented fins in the other species). From *S. diomedeanus*, *S. oculellus* differs in caudal-fin-ray count (12 vs. 10 in *S. diomedeanus*), and lacks a pupillary operculum (present in *S. diomedeanus*). In *S. oculellus*, the dorsal and anal fins have an alternating series of somewhat rectangular-shaped, pigmented blotches and unpigmented areas beginning in the mid-body region and continuing posteriorly inclusive of the caudal fin, whereas in *S. diomedeanus* the dorsal and anal fins have fewer, nearly spherical spots only in the posteriormost portions of these fins, and the caudal fin usually lacks pigmented spots completely (only rare specimens have a spot present on the caudal fin).

There are seven eastern Pacific *Symphurus* with similar ID patterns, comparable fin-ray counts, or pigment patterns reminiscent of those observed in *S. oculellus*. Of these seven species, only *S. chabanaudi* and *S. elongatus* are similar to *S. oculellus* in lacking a pupillary operculum. Many meristic features of *S. oculellus* completely overlap those of the eastern Pacific

S. chabanaudi. *Symphurus oculellus* differs from *S. chabanaudi*, however, in lacking the 4–8 small but well-developed scales on the blind sides of the dorsal and anal fin rays prominent in *S. chabanaudi* specimens, especially those larger than 60 mm; in having a somewhat smaller eye (1.2–1.9, $\bar{x}$ 1.5 SL in *S. oculellus* vs. 1.7–2.3, $\bar{x}$ 1.9 SL), and *S. oculellus* has a well-developed fleshy ridge on the ocular-side lower jaw (absent in *S. chabanaudi*). The posterior extension of the jaws in *S. oculellus* extends to the vertical line through the posterior margin of the eye, and in many specimens the jaws actually extend slightly beyond the posterior margin of the eyes, whereas in *S. chabanaudi* the posterior extension of the jaws reaches only to a vertical line through the rear margin of the pupil or the rear margin of the lower eye. *Symphurus oculellus* also differs from *S. chabanaudi* in the relative frequencies of specimens possessing 1-5-3 and 1-4-3 ID patterns. *Symphurus chabanaudi* has a much higher frequency of occurrence of the 1-5-3 ID pattern (50% of individuals examined) compared with only 30% with a 1-4-3 pattern. In contrast, 40 of 45 (89%) of the *S. oculellus* examined had a 1-4-3 pattern and only one specimen possessed a 1-5-3 pattern.

Symphurus chabanaudi also differs from *S. oculellus* in that this species generally has about nine wide, dark-brown crossbands compared with the more numerous (10–14, usually 10–12), narrower bands in *S. oculellus*. In addition, in *S. oculellus* the posterior two-thirds of the dorsal and anal fins usually have an alternating series of blotches and unpigmented areas, whereas in *S. chabanaudi* the posterior one-third of the dorsal and anal fins, and the caudal fin, are usually uniformly dark-brown or black without alternating blotches and unpigmented areas.

There is almost complete overlap in fin-ray and vertebral counts between those of *S. oculellus* and those of *S. elongatus*; however, these species are otherwise distinct. *Symphurus oculellus* has prominent crossbands on the body and a dark blotch on the ocular-side opercle, whereas in *S. elongatus* the body is uniformly pigmented without crossbands, and a prominent blotch on the ocular-side opercle is wanting.

The remaining five eastern Pacific species with meristics comparable to those observed in *S. oculellus* include *S. leei*, *S. atricaudus*, *S. melanurus*, *S. williamsi*, and *S. undecimplerus*. These species, in contrast to *S. oculellus*, possess a pupillary operculum, and none features the pigmented blotch found on the ocular-side opercle in *S. oculellus*. *Symphurus oculellus* differs further from *S. undecimplerus* in caudal-fin-ray number (12 vs. 11); is distinguished from *S. melanurus* and *S. williamsi* in having the dorsal and anal fins with an alternating series of pigmented blotches and unpigmented areas (versus dorsal and anal fins without an alternating series of pigmented blotches and unpigmented areas in these other species); is readily distinguished from *S. leei* in having an unpigmented peritoneum (versus black in *S. leei*) and in having the head length smaller than body depth (nearly equal to body depth in *S. leei*); and differs from *S. atricaudus* in lacking the small ctenoid scales on the ocular-side dorsal and anal fin rays characteristic of that species.

Material examined 69 specimens (75.8–189 mm SL).

Counted and measured (14 specimens, 75.8–164 mm SL). **Holotype**: USNM 159606; female, 144 mm SL; Surinam (6°24′N, 55°00′W); 27 m; 11 May 1957. **Paratypes. Guyana**: BMNH 1950.5.15: 51; (139); off Georgetown. FMNH 86365; (148); 7°05′N, 57°12′W; 33 m; 1 Sep 1958. FMNH 88846; (132); 6°54′N, 57°47′W; 18 m; 25 Mar 1963. **Surinam**: USNM 159559; (75.8); 6°04′N, 54°51′W; 70 m; 13 May 1951. ZMA 111.212; (158); 5°15′N, 55°15′W; 12 m; 13 Oct 1969. **French Guiana**: UMML 12254; (141); 6°17′N, 53°35′W; 40 m; 21 Feb 1963. USNM 313518; 2(143–151); 6°12′N, 53°23′W; 46 m; 1 Jul 1972. UMML 11549; (156); 5°57′N, 52°18′W; 70 m; 22 Feb 1963. UMML 12262; (148); 5°24′N, 51°34′W; 64 m; 23 Feb 1963. ZMA 111.234; (140); 3°45′N, 51°45′W; 40 m; 16 Nov 1969. **Brazil**: FMNH 86362; (155); 1°57′N, 48°15′W; 48 m; 17 Nov 1957. FMNH 100385; (164); 1°57′N, 48°12′W; 55 m; 14 Nov 1957.

Counted (30 paratypes, 14 lots). **Guyana**: BMNH 1961.9.4:117; (189). BMNH 1961.9.4:118; (163). UMML 34335; (136); 7°42′N, 57°32′W; 27 m; 15 Jul 1968. **Surinam**: GCRL 3836; 5(130–165); 6°56′N, 54°05′W; 2 May 1969. UMML 12249; (143); 6°18′N, 55°11′W; 18 m; 20 Feb 1963. ZMA 111.228; 1; 5°15′N, 55°15′W; 12 m; 10 Oct 1969. FMNH 90552; 2(142–147); Surinam; 18 m; 1957. FMNH 90553; (144); Surinam; 110 m; 3 May 1957. FMNH 91368; (141); Surinam; 1957. **French Guiana**: FMNH 100386; 7(154–180); 6°03′N, 52°22′W; 65 m; 13 Sep 1958. FMNH 90085; 5(163–180); 5°46′N, 52°02′W; 70 m; 12 Nov 1957. FMNH 86397; (130); 5°05′N, 52°14.5′W; 20 m; 23 May 1957. **Brazil**: FMNH 100387; 2(140–155); 2°29′N, 48°54′W; 86 m; 15 Nov 1957. USNM 159541; (150); 2°29′N, 48°55′W; 42 m; 15 Nov 1957.

Other non-type material examined (25 specimens, 14 lots). **Guyana**: UMML 34364; (152); 7°00′N, 57°08′W; 26 m; 15 Jul 1968. **Surinam**: UMML 12498; (158); 7°01′N, 54°21′W; 64 m; 21 Feb 1963. FMNH 90223; (135); 6°54′N, 54°47′W; 18 m; 25 Mar 1953. UMML 34334; 2(104–140); 6°25′N, 55°04′W; 7 m; 10 Jul 1968. FMNH 91109; (151); 6°24.5′N, 55°02.5′W; 27 m; 11 May 1957. USNM 159602; 2(82.2–94.8); 6°23′N, 55°05.5′W; 27 m; 11 May 1957. USNM 313515; 3(136–152); 6°21′N, 54°28′W; 28 m; 29 Jun 1972. UMML 12310; 3(139–142); 6°11′N, 55°39′W; 15 m; 19 Feb 1963. **French Guiana**: UMML 13301; 6(111–175); 6°00′N, 52°27′W; 64 m; 22 Feb 1963. UMML 13307; (166); 5°29′N, 51°37′W; 64 m; 23 Feb 1963. UF 83997; (143); 5°05′N, 51°58′W; 45 m; 11 Dec 1977. USNM 313516; (147); 4°47′N, 51°37′W; 33 m; 5 May 1975. UMML 34336; (160); off Cayenne; F. Berry, Station 10, 12. **Brazil**: UMML 12265; (150); 2°20′S, 40°24′W; 40 m; 12 Mar 1963.

Symphurus caribbeanus, new species
Figures 2, 4e, 5, 6d

Synonymy

Symphurus plagusia plagusia. Ginsburg 1951:220 (in part) (Fox Bay, Panama; specimens in USNM 81654 included in account of *S. p. plagusia*).

Symphurus plagusia. Austin and Austin 1971:38 (in part) (Guayanilla, Puerto Rico; food habits; nine specimens from UPRM 2926 belong to the new species).

Diagnosis A *Symphurus* with the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal fin rays; unpigmented peritoneum; relatively large eye (82–110 HL); no fleshy ridge on ocular-side lower jaw; without a pupillary operculum; no small ctenoid scales on the blind sides of the dorsal and anal fin rays; dorsal fin rays 89–96, usually 92–96; anal fin rays 74–80; total vertebrae 48–51, usually 49–50; 78–89 scales in longitudinal series; relatively short jaws usually extending to the vertical line through the posterior margin of pupil of lower eye or occasionally extending to the vertical through posterior margin of lower eye; dorsal fin origin usually reaching, or occasionally slightly anterior to, vertical line through front margin of upper eye; ocular surface dark-brown to almost yellow; usually with 10–15 narrow, irregularly complete, sharply contrasting, dark-brown crossbands on head and trunk; outer surface of ocular-side opercle without dark blotch; inner lining of opercle and isthmus heavily pigmented on ocular side, unpigmented on blind side; entire dorsal and anal fins with alternating series of blotches and unpigmented areas.

Table 18
Summary of morphometrics expressed in thousandths of standard length (except SL in mm) for the holotype (USNM 313487) and 20 paratypes of *Symphurus caribbeanus*. (Abbreviations defined in Methods section.)

	Holotype	Paratypes		
Character	(USNM 313487)	Range	Mean	SD
SL	100.5	40.1–121.9	84.5	22.40
BD	317	277–320	300.6	12.14
PDL	34	29–48	36.2	5.45
PAL	219	191–261	223.0	15.89
DBL	966	952–972	964.3	5.70
ABL	792	751–820	781.0	18.89
PL	62	51–75	63.2	6.56
PA	45	35–63	47.6	6.62
CFL	106	87–116	102.4	7.56
HL	194	185–224	199.2	10.94
HW	239	220–268	240.0	11.03
POL	123	119–143	133.6	6.72
SNL	45	36–54	43.5	4.92
UJL	49	37–56	46.2	4.85
ED	20	17–22	19.4	1.56
CD	52	43–64	51.8	5.06
UHL	141	152–184	164.6	32.23
LHL	112	84–111	98.6	26.53

Description A medium-sized tonguefish attaining maximum lengths of approximately 122 mm SL. ID pattern usually 1-4-3 (67/82), less frequently 1-3-3 (8), 1-3-4 (23), or 1-4-4 (2) (Table 1). Caudal fin rays usually 12 (78/82), less frequently 11, 10, or 13 (Table 2). Dorsal fin rays 89–96, usually 92–96 (Table 3). Anal fin rays 74–80 (Table 4). Total vertebrae 48–51, usually 49–50 (75/79) (Table 5); abdominal vertebrae 3+6. Hypurals 4. Longitudinal scale rows 78–89 (Table 6). Scale rows on head posterior to lower orbit 17–22, usually 19–21 (Table 7). Transverse scales 36–44 (Table 8).

Proportional measurements appear in Tables 18 and 19. Body relatively deep (277–320 SL, $\bar{x}$ 301); with greatest depth in anterior one-third of body followed by relatively rapid taper posteriorly. Preanal length 191–261 SL, $\bar{x}$ 223; somewhat shorter than body depth. Head relatively short (185–224 SL, $\bar{x}$ 199); considerably shorter than body depth. Head relatively wide (220–268 SL, $\bar{x}$ 240); greater than head length (HW/HL 1.1–1.3, $\bar{x}$ 1.2); lower head lobe (84–111 SL, $\bar{x}$ 99) considerably narrower than upper head lobe (152–184 SL, $\bar{x}$ 165). Lower opercular lobe of ocular side (241–348 HL, $\bar{x}$ 292) considerably wider than upper opercular lobe (162–277 HL, $\bar{x}$ 199). Postorbital length 119–143 SL, $\bar{x}$ 134. Snout moderately long (193–255 HL, $\bar{x}$ 218) and pointed (Fig. 4e), covered with small ctenoid scales. Anterior nostril usually not reaching anterior margin of lower eye when depressed posteriorly. Dermal papillae well developed on blind side of snout and chin regions, but not particularly dense. Jaws relatively short; upper jaw length 195–253 HL, $\bar{x}$ 231; posterior extension of maxilla usually reaching to vertical line through posterior margin of pupil or occasionally posterior margin of lower eye. Ocular-side lower jaw without distinct, fleshy ridge near posterior margin (Fig. 4e). Chin depth 227–305 HL, $\bar{x}$ 260. Lower eye moderately large (82–110 HL, $\bar{x}$ 97); upper eye usually slightly anterior to lower eye; eyes not covered with scales; usually 1–3 small ctenoid scales in narrow interorbital space. Pupillary operculum absent. Length of dorsal fin base 952–972 SL, $\bar{x}$ 964. Dorsal fin origin (Fig. 4e) usually reaching, or occasionally slightly anterior to, vertical line through front margin of upper eye; predorsal length 29–48 SL, $\bar{x}$ 36. Length of anal fin base 751–820 SL, $\bar{x}$ 781. Scales absent on blind sides of dorsal and anal fin rays. Pelvic fin relatively short, 51–75 SL, $\bar{x}$ 63; longest pelvic fin ray usually reaching base of first or

Table 19
Summary of morphometrics expressed as thousandths of head length (except HW/HL) for the holotype (USNM 313487) and 20 paratypes of *Symphurus caribbeanus*. (Abbreviations defined in Methods section.)

	Holotype	Paratypes		
Character	(USNM 313487)	Range	Mean	SD
HW/HL	1.2	1.1–1.3	1.2	0.06
POL	636	632–744	671.6	28.72
SNL	231	193–255	218.4	18.47
UJL	251	195–253	231.3	15.96
ED	103	82–110	97.4	7.18
CD	267	227–305	259.8	19.74
OPLL	359	241–359	291.8	32.23
OPUL	236	162–274	199.4	27.34
UHL	728	725–973	828.0	57.84
LHL	580	437–592	495.7	39.42

occasionally second anal fin ray; pelvic to anal fin distance 35–63 SL, $\bar{x}$ 48. Posteriormost pelvic fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly almost to origin of anal fin base (membrane torn in most specimens). Caudal fin relatively short, 87–116 SL, $\bar{x}$ 102.

Teeth well developed on blind-side jaws. Upper and lower jaws on ocular side usually with small patch of teeth covering only anterior one-third of jaw, or lacking teeth altogether.

Scales moderate in size, strongly ctenoid on both sides of body.

Pigmentation Pattern of body pigmentation generally similar for both sexes at all sizes, but mature males with more intense pigmentation on body and posterior portions of dorsal and anal fins. Ocular surface dark-brown to almost yellow; usually with 10–15 narrow, irregularly complete, sharply contrasting, darker-brown crossbands on head and trunk. Crossbands not continued onto dorsal and anal fins. Anteriormost band on head immediately posterior to eyes. Second band crossing head just anterior to opercular opening. Crossbands on trunk variable in number, usually 3–6 scale rows in width. First band crossing body immediately posterior to opercular opening. Posteriormost band slightly anterior to caudal fin base, irregularly complete. Blind side off-white. Peritoneum unpigmented. Outer surface of ocular-side opercle with general background pigmentation. Dorsal margin of ocular-side opercle sometimes with dusky blotch due to dark pigmentation of inner lining of operculum showing through to outer surface. Inner lining of opercle and isthmus heavily pigmented on ocular side; unpigmented on blind side. Slight band of pigment on ocular-side upper lip; ocular-side lower lip frequently spotted but without definite band of pigment.

Pigmentation of dorsal and anal fins generally similar in both sexes, but usually more intense in males. Except for anteriormost portion of dorsal fin, entire dorsal and anal fin with alternating series of dark blotches and unpigmented areas. Blotches variable in shape, most frequently nearly rectangular; extending from base almost to distal tip of fin rays; blotches usually covering 2–5 fin rays alternating with 2–4 lightly-pigmented fin rays. Caudal fin either uniformly darkly-pigmented, or with alternating series of pigmented blotches and unpigmented areas throughout length of fin.

Size and sexual maturity Adult *S. caribbeanus* range in size from approximately 71 to 122 mm SL, and this species is one of the smallest members of the *S. plagusia* complex. Size-related life-history information is derived from data taken from 89 specimens. Males and females attain similar sizes. The largest fish measured was a gravid female (122 mm SL); largest male was (120 mm SL).

There were 44 males (52.9–122 mm SL), 39 females (55.6–122 mm SL), and 6 immature fish (24.4–43.8 mm SL) among material examined. Based on reproductive stages of females, this species matures at 70–80 mm SL (Fig. 2). There were 30 mature females ranging in size from 71.8 to 122 mm SL. All females larger than 80 mm SL were mature. The smallest mature female (71.8 mm SL) was unusual because six of seven others in this size range had undeveloped gonads.

Of 39 females, nine, ranging from 55.6 to 79.1 mm SL, were immature with only partially elongate ovaries. The smallest immature females (55.6, 56.9 mm SL) had only partially elongate ovaries, whereas some larger immature females (58.1–79.1 mm SL) had more developed ovaries but were without obviously developing ova.

Etymology This species is named after its area of occurrence in reference to its common but apparently restricted distribution to habitats within the Caribbean Sea.

Geographic distribution (Fig. 5) Widely distributed in the Caribbean Sea. *Symphurus caribbeanus* has been collected along coastal margins of central and northern South America and off islands fringing the Caribbean Sea. Islands where this species has been collected include St. Martin and Cuba, but most specimens examined were taken at Puerto Rico and Haiti. This species has been collected at coastal locations in Nicaragua, Costa Rica, and Panama along

Central America, and also along the Caribbean coast of Colombia.

Bathymetric distribution *Symphurus caribbeanus* inhabits shallow water. Of 94 specimens for which depth information was available, the majority (78/94, 83%) were collected in 20 m or less (Table 11), and approximately half were collected in waters shallower than 10 m. All life stages are represented among the shallowest collections. The deepest capture (29 m) is for one lot (UMML 34341) comprising 16 individuals.

Ecology Other than depth of occurrence and geographic distribution, little is known about ecological requirements of this species. Austin and Austin (1971) included nine specimens of *S. caribbeanus* in their survey of feeding habits of fishes inhabiting mangrove areas in southwestern Puerto Rico. These specimens, ranging in size from 30 to 104 mm SL, had fed mostly on polychaetes and small, benthic crustaceans, and individuals collected at night had undigested food in their stomachs, suggesting nocturnal feeding.

Comparisons Among Atlantic members of the *S. plagusia* complex, *S. caribbeanus* most closely resembles and occurs sympatrically with *S. plagusia* and juvenile and subadult *S. tessellatus*. There is overlap also in some meristic features of *S. caribbeanus* and *S. civitatium*, but these species are otherwise quite distinct. *Symphurus caribbeanus* differs considerably from *S. oculellus*. Differences between *S. caribbeanus* and these other species were discussed previously in "Comparisons" sections under the accounts for *S. plagusia*, *S. civitatium*, *S. tessellatus*, and *S. oculellus*.

Meristic values of *S. caribbeanus* overlap those of 11 other Atlantic species of *Symphurus*. *Symphurus caribbeanus* is readily distinguished from six deep-water Atlantic species with similar meristic values (*S. marginatus* (Goode and Bean) and *S. piger*, occurring in the Gulf of Mexico and Caribbean; two western North Atlantic species, *S. pusillus* and undescribed species C of Munroe (1987); the western South Atlantic *S. ginsburgi* Menezes and Benvegnú; and the eastern Atlantic *S. nigrescens*) in ID pattern (1-4-3 vs. 1-3-2 in the others) and peritoneal pigmentation (unpigmented versus dark-black, visible through both sides of abdominal wall in the others). *Symphurus caribbeanus* differs from two diminutive eastern Atlantic species, *S. lubbocki* and *S. reticulatus*, in ID pattern (1-4-3 vs. 1-3-2), dentition on ocular-side jaws (absent or reduced in *S. caribbeanus* versus complete row in the others), and longitudinal scale counts (78–89 in *S. caribbeanus* versus 95 or more in *S. lubbocki* and *S. reticulatus*). *Symphurus caribbeanus* differs from the eastern Atlantic *S. normani* in ID pattern (1-4-3 vs. 1-3-3), peritoneal pigmentation (unpigmented versus spotted in *S. normani*), and *S. caribbeanus* lacks the small ctenoid scales on the blind sides of the dorsal and anal fin rays that are present in *S. normani*. *Symphurus caribbeanus* differs further from the western South Atlantic *S. trewavasae* and *S. kyaropterygium* Menezes and Benvegnú, in caudal-fin-ray count (12 vs. 10) and ID pattern (1-4-3 vs. 1-3-3 in *S. trewavasae*, 1-4-2 in *S. kyaropterygium*). *Symphurus caribbeanus* also lacks the pupillary operculum and fin membrane ostia characteristic of *S. kyaropterygium*.

Three shallow-water, western Atlantic species—*S. diomedeanus*, which occurs in sympatry with *S. caribbeanus*, and the allopatric *S. plagiusa* and *S. urospilus* Ginsburg—have meristic features similar to those of *S. caribbeanus*. *Symphurus caribbeanus* differs from these species in caudal-fin-ray count (12 vs. 10 in *S. diomedeanus* and *S. plagiusa*, 11 in *S. urospilus*) and pigmentation of the vertical fins. The vertical fins of *S. caribbeanus* have an alternating series of blotches and unpigmented areas and the caudal fin lacks an ocellated spot, unlike the vertical fins in *S. diomedeanus* which have fewer, nearly spherical spots; or those of *S. plagiusa* and *S. urospilus*, that are uniformly pigmented without darkly-pigmented blotches throughout their lengths; or the caudal fin in *S. urospilus* that has an ocellated spot. From *S. plagiusa*, *S. caribbeanus* further differs in the absence of a black opercular spot and the small ctenoid scales on the blind-side dorsal and anal fins characteristic of *S. plagiusa*. *Symphurus caribbeanus* is further distinguished from *S. diomedeanus* and *S. urospilus* in lacking a pupillary operculum (present in the others).

Meristic values of *S. caribbeanus* overlap those of six eastern Pacific species possessing either a 1-4-3 or 1-5-3 ID pattern, including *S. leei*, *S. atricaudus*, *S. melanurus*, *S. williamsi*, *S. fasciolaris*, and *S. melasmatotheca*. *Symphurus caribbeanus* differs from all of these species in lacking a pupillary operculum (present in the others). Of all these species, *S. caribbeanus* appears most similar to *S. williamsi* but differs in lacking small ctenoid scales on the blind sides of the dorsal and anal fin rays (present in *S. williamsi*) and in having pigmented blotches in the dorsal and anal fins (versus dorsal and anal fins without blotches in *S. williamsi*). *Symphurus caribbeanus* also differs from *S. atricaudus* in lacking small ctenoid scales on the ocular-side dorsal and anal fin rays and in having an alternating series of pigmented blotches in the dorsal and anal fins (scales present and fins uniformly pigmented in *S. atricaudus*). From *S. melanurus*, *S. caribbeanus* differs in that *S. melanurus* possesses a fleshy ridge on the ocular-side lower jaw and the first dorsal fin ray reaches a vertical equal with or anterior to the anterior margin of the upper eye, whereas *S. caribbeanus* lacks a fleshy

ridge on the ocular-side lower jaw and the first dorsal fin ray is usually placed posterior to the vertical through the front margin of the upper eye. These two species are further distinguished by the fewer scales in a longitudinal series (78–89 in *S. caribbeanus* vs. 89–108 in *S. melanurus*), the lightly-pigmented inner lining on the blind-side opercle (versus darkly-pigmented inner lining on the blind-side opercle in *S. melanurus*), and because the posterior dorsal and anal fins and the caudal fin of *S. caribbeanus* have an alternating series of pigmented blotches and unpigmented areas (versus progressive darkening in posterior dorsal and anal fins without alternating series of blotches and unpigmented areas in *S. melanurus*). *Symphurus caribbeanus* differs from *S. fasciolaris* and *S. melasmatotheca* in possessing 12 caudal fin rays (versus 10 and 11 in *S. fasciolaris* and *S. melasmatotheca*, respectively) and in lacking an ocellated spot on the caudal fin (present in *S. fasciolaris*) or pigmented peritoneum (present in *S. melasmatotheca*). From *S. leei*, *S. caribbeanus* is further distinguished in having the head length considerably smaller than the body depth (head length nearly equal with body depth in *S. leei*), in its smaller eye (17–22 SL vs. 22–27 SL in *S. leei*), and in having an unpigmented peritoneum (black in *S. leei*).

Material examined 100 specimens (24.4–122mm SL).

Counted and measured (21 specimens, 40.1–122mm SL). **Holotype**: USNM 313487; male, 100.5mm SL; Mayaguez Bay, Puerto Rico; 1966; Collected by J.S. Ramsey. **Paratypes. Haiti**: FMNH 61574; (40.7); Port-au-Prince Bay; 12 Sep 1953. **Netherlands Antilles**: UMML 5297; (40.1); St. Martin; 1m; 2 Jul 1959. **Puerto Rico**: UPRM 740; 2(120–122); Río Anasco; 1–2 Jul 1953. UPRM 1588; (98.0); Mayaguez; Mar 1962. UPRM 2926; 8(58.1–97.9); Guayanilla; 23 Jul 1968. ANSP 118553; (69.8); Puerto Rico; 25 Jan 1971. **Colombia**: UMML 30087; 6(88.7–98.1); 8°44.5–45.6′N, 76°52.71′W; 4m; 12 Jul 1966.

Counted (2 **paratypes**, 1 lot)—**Colombia**: USNM 313513; 2(102.8–116.7); Bajo-Sabanilla, off Barranquilla; 8 Sep 1969. (60 **non-type specimens**, 10 lots)—**Puerto Rico**: ANSP 115601; 7(43.3–82.5); Puerto Yabucoa; 12–13 Jul 1969. UPRM 736; (95.8); Río Anasco; 17 Aug 1951. UPRM 740; 8(90.0–122); Río Anasco; 1–2 Jul 1953. **Cuba**: MCZ 11200; (71.8); 1851. **Haiti**: UF 83998; 10(80.7–95.4); 2km NW of Port Salut; sandy beach near eelgrass bed; 1m; 7 Apr 1979. UMML 34337; 3(95.8–110). **Nicaragua**: UMML 34338; 2(79.1–94.3); 12°16′N, 83°31′W; 12m; 28 Jan 1971. **Panama**: UMML 34339; (115); 8°49′N, 81°13′W; 18m; 21 Jul 1966. UMML 34340; 26(24.4–117); 9°48′N, 82°50′W; 19m; 26 Jan 1971. USNM 313514; (46.2); Colon; 5 Jan 1911.

Other non-type material examined (17 specimens, 2 lots). **Cuba**: MCZ 25982; (108.7). **Costa Rica**: UMML 34341; 16(52.9–117); 10°40′N, 83°29′W; 29m; 27 Jan 1971.

Comparative life histories and distributions

In addition to morphological and pigmentation differences among Atlantic members of the *S. plagusia* complex, significant differences among members of this species complex are evident in geographic ranges, ecologies (primarily bathymetric occurrence), and life-history traits, including adult sizes and minimal sizes at sexual maturity. With the exception of *S. civitatium*, which occurs allopatrically in coastal seas off the southeastern United States and northern Mexico, these species occur in the Caribbean Sea and South Atlantic Ocean. Two species, *S. plagusia* and *S. tessellatus*, have extensive and sympatric distributions, ranging throughout insular and coastal locations from the northern Caribbean Sea to as far south as Rio de Janeiro, Brazil, for *S. plagusia* and to northern Uruguay for *S. tessellatus*. The geographic ranges of both *S. plagusia* and *S. tessellatus* completely overlap those of *S. caribbeanus* and *S. oculellus*, species with more restricted distributions. *Symphurus caribbeanus* occurs throughout insular and coastal areas in the Caribbean, with its southernmost occurrence in the western Caribbean off Colombia. *Symphurus oculellus* has the most restricted distribution of the species complex, occurring on the continental shelf along the northern coast of tropical South America north of 5°S from approximately 40°–60°W longitude.

Overall, members of the *S. plagusia* complex are generally shallow-water species, inhabiting nearshore and coastal seas usually shallower than 80m (Table 11). Only rarely have individuals been collected deeper than 80m, and none have been taken at depths greater than 110m. In contrast, of the other eleven Atlantic species possessing 12 caudal fin rays (all have a 1-3-2 ID pattern), seven species usually inhabit much deeper waters on the continental shelf and upper continental slope, ranging from 35 to 700m, with centers of abundance usually between 100 and 350 m (Munroe 1987). Exceptional to this observation are four diminutive species (*S. arawak* Robins and Randall, *S. rhytisma* Böhlke, *S. lubbocki*, and *S. reticulatus*), which occur on shallow substrates adjacent to coral reefs.

Although three of the five Atlantic species of the *S. plagusia* complex are known to have overlapping geographic ranges, the species do not occur syntopically at all life-history stages, especially with respect to bathymetric occurrences (Table 11). Three of the five Atlantic members of the *S. plagusia* complex, *S. plagusia*, *S. tessellatus*, and *S. caribbeanus*, occur syntopically at some stage in their life history in shallow waters of the Caribbean. Juveniles of all three species have been taken exclusively in beach seine and otter

trawl collections in shallow-water (<10 m) estuarine and mudflat habitats. However, striking differences are apparent in how these species utilize inshore habitats. In these habitats, juvenile *S. tessellatus* are collected with all life history stages of *S. plagusia* and *S. caribbeanus*. Adult *S. tessellatus*, however, apparently undergo an ontogenetic migration from shallow, nearshore habitats to deeper waters further offshore (11–80 m) on the continental shelf. In contrast, although a small number of *S. caribbeanus* and *S. plagusia* have been taken as deep as 30–40 m on the continental shelf, these were isolated captures of large adults (>110 mm SL). The majority of *S. plagusia* and *S. caribbeanus* (80% and 83%, respectively), including all juveniles examined, were collected in waters shallower than 20 m. Most specimens were taken by beach seine and small otter trawls at depths shallower than 10 m in nearshore mudflats, mangrove habitats, and estuarine locations.

Symphurus oculellus, although occurring sympatrically with *S. plagusia* and *S. tessellatus* (see Figures 3 and 5), apparently has a different life history than these other species. *Symphurus oculellus* inhabits deeper waters than the others (Table 11), spanning an overall bathymetric range of 7–110 m, but being captured most frequently in waters deeper than 20 m (78% collected deeper than 20 m). *Symphurus oculellus*, including juveniles as small as 76 mm SL, have been collected in neritic waters deeper than 7 m and none have been taken from estuarine habitats, contrary to *S. plagusia* and *S. tessellatus*. However, estuarine environments in the geographic range of *S. oculellus* along northeastern South America have not been as thoroughly sampled as have those nearshore habitats occupied by *S. plagusia* and juvenile *S. tessellatus* in the northern Caribbean and southern Brazilian areas. *Symphurus civitatium*, the northernmost-occurring species, is the only Atlantic species with a distribution allopatric to those of other members of this species group. Adult *S. civitatium* are very abundant in collections and, although inhabiting a wide depth range (1–73 m), are more commonly captured between 11 and 45 m on the inner continental shelf where approximately 91% (199/216) of the specimens examined in the present study were collected (Table 11). It is unusual for adult *S. civitatium* to occur in habitats deeper or shallower than this depth range. For example, the deepest captures of this species were made at 73 and 62 m, where a single fish was taken each time, and of four fish collected in waters shallower than 10 m, only one was an adult and three others were small juveniles (<35 mm SL). Little is known concerning early-life-history stages of *S. civitatium*. Few juveniles have been collected, but all of these were taken at inshore locations. The occurrence of early-life-history stages in nearshore waters suggests a life-history pattern similar to that of *S. tessellatus*, where adults occur in deeper waters on the inner continental shelf and juveniles inhabit estuarine or nearshore nurseries. However, distribution data for this species, especially for early juveniles, are too incomplete to estimate how regularly this species utilizes inshore waters as nurseries. Further investigation is needed on whether recent captures of early juveniles in estuarine environments represent isolated occurrences of this species or its normal life-history pattern.

Among *Symphurus*, members of the *S. plagusia* complex are medium- to large-sized tonguefishes, ranging in maximum lengths from 122 mm SL for *S. caribbeanus* to 220 mm SL for *S. tessellatus*, the second largest species of tonguefish in the Atlantic (only *S. jenynsi* from the southern South Atlantic exceeds these sizes) and third largest in the genus (Fig. 2). *Symphurus caribbeanus* and *S. plagusia* are the smallest of the five Atlantic species of this complex (122 and 130 mm SL, respectively), and also mature at the smallest sizes (70–80 mm SL for *S. caribbeanus*; 80 mm SL for *S. plagusia*). *Symphurus civitatium* is only slightly larger, attaining maximum lengths of ~152 mm SL and maturing at sizes slightly greater than 90 mm SL. *Symphurus oculellus* and *S. tessellatus* are the largest Atlantic species in this complex, attaining maximum sizes of 189 and 220 mm SL, respectively. Not surprisingly, these larger-sized species also mature at somewhat larger sizes. Female *S. oculellus* mature at about 110 mm SL and female *S. tessellatus* at 104–120 mm SL.

Comparisons of ecological and life-history parameters, like those above, supplement and corroborate systematic determinations based on morphological evidence. However, in the absence of a cladistic hypothesis, the value of these ecological comparisons, especially concerning historical relationships, either of the species complex within the genus or of the individual species comprising the *S. plagusia* complex, cannot be fully assessed. Further study, based on shared derived characters using outgroup comparisons or ontogeny, is needed before intrageneric relationships of the species complex and interrelationships of its members can be determined to better understand trends in the evolution of life-history attributes of these tonguefishes.

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Abstract.–Samples of yellowfin tuna *Thunnus albacares* from five different areas of the Pacific Ocean, Mexico, Ecuador, Australia, Japan, and Hawaii, collected during January to May of 1988, were examined for geographic variation in morphometric characters and gill-raker counts. The Kruskal-Wallis test indicated a significant difference in the total gill-raker counts among areas. The morphometric data were adjusted by allometric formulae to remove size effects. The overall percent-correct classification rate for the five groups from the stepwise discriminant analysis, based on 12 adjusted morphometric characters, was 77.6%. This is 72.0% (Cohen's kappa statistic) better than would have occurred by chance. These results indicate significant meristic and morphological differences of yellowfin tuna from these areas, which suggests that fish from these areas represent separate groups.

Geographic Variation in Morphometric Characters and Gill-Raker Counts of Yellowfin Tuna *Thunnus albacares* from the Pacific Ocean

Kurt M. Schaefer

Inter-American Tropical Tuna Commission, Scripps Institution of Oceanography
8604 La Jolla Shores Drive, La Jolla, California 92037

Yellowfin tuna *Thunnus albacares* is an epipelagic species found worldwide in tropical and subtropical oceanic regions, with a nearly continuous distribution in the Pacific Ocean from roughly 40°N to 40°S (Collette and Nauen 1983). The large-scale industrial fisheries for tuna in the Pacific Ocean landed an estimated 471 thousand metric tons of yellowfin tuna in 1985 (Joseph 1987). Fundamental to the proper management of yellowfin tuna is the elucidation of population structure. The interactions among existing, expanding, or developing fisheries on this resource cannot be assessed without this knowledge.

Morphometric studies have provided results useful for identifying marine fish stocks and describing their spatial distributions (Ihssen et al. 1981, Winans 1987). Morphometric characters, used extensively in the analysis of population structure of yellowfin tuna, indicate that there are at least three groups in the Pacific Ocean. Godsil (1948) and Godsil and Greenhood (1951) identified four stocks of yellowfin tuna in the Pacific (Japan, Hawaii, Peru, and the northeastern Pacific) from morphometric characters. Morphometric data indicate that yellowfin tuna from southeastern Polynesia, Hawaii, and Central America are different stocks (Schaefer 1955). Kurogane and Hiyama (1957) concluded from morphometric data that there are three stocks in the Pacific: western, central, and eastern. Royce (1964), however, concluded that there is an apparent cline in morphometric characters along the equator from off Costa Rica to the Caroline Islands. Suzuki et al. (1978) reviewed fisheries and biological data, including morphometric data, and concluded that there are at least three relatively independent stocks: western, central, and eastern Pacific. More recently, Schaefer (1989) showed morphometric differences between yellowfin tuna from north and south of 15°N–20°N in the eastern Pacific Ocean. With the exception of Schaefer's (1989) study, previous investigations primarily utilized univariate analyses of morphometric characters. Although geographic variation in yellowfin tuna morphology can be demonstrated in this manner, univariate analyses of single characters do not permit the classification of individual fish into discrete groups or stocks.

The objectives of the present study were to (1) assess and describe geographic variation in morphological characters and gill-raker counts of yellowfin tuna from five widely-scattered locations of the Pacific basin, (2) test the hypothesis of morphometrically distinguishable northern and southern groups in the eastern Pacific, and (3) identify the

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best set of characters for group separation. I examined gill-raker counts because this meristic character appeared useful in separating groups of Pacific yellowfin tuna (Godsil and Byers 1944, Schaefer 1955). Rather than using the term "stock(s)," since it is not known whether there is a genetic component to the differences observed, I use the term "group(s)," as defined by Marr (1957), because this avoids the technicality of the degree to which genetics are involved in the differences observed.

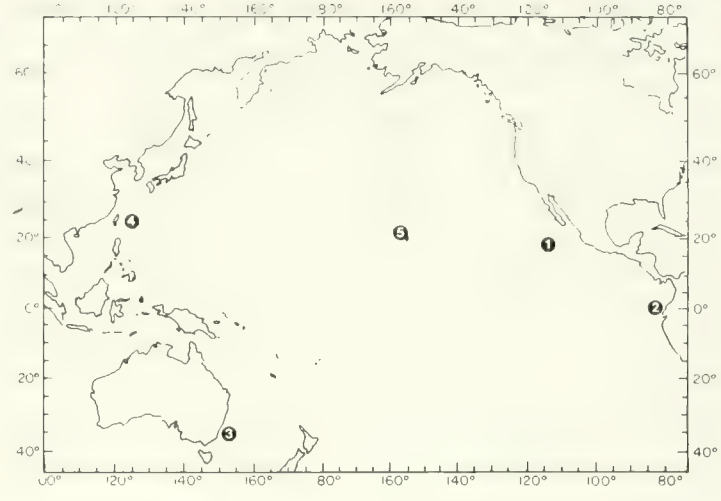


Figure 1
Sampling locations in the Pacific Ocean for yellowfin tuna: (1) Revillagigedo Islands, Mexico; (2) Manta, Ecuador; (3) New South Wales, Australia; (4) Ishigaki, Japan; and (5) Oahu, Hawaii.

Materials and methods

Sampling and data collection

Yellowfin tuna were captured by baitboats, trollers, or sportfishing boats during January to May 1988, from five localities in the Pacific Ocean: the Revillagigedo Islands, Mexico; Manta, Ecuador; New South Wales, Australia; Ishigaki, Japan; and Oahu, Hawaii (Fig. 1). These locations were selected to optimize spatial coverage within the distribution of the surface and longline fisheries for yellowfin tuna in the Pacific. Samples ranged from 66 to 105 individuals per location (Table 1), and included fish from at least four schools from each area.

Table 1
Summary statistics for total length in millimeters, by area, for 452 yellowfin tuna.

Sample	n	Mean	SD	Min.	Max.
Mexico	101	635.4	151.7	444	983
Ecuador	80	532.9	101.4	431	789
Australia	66	853.9	49.4	690	990
Japan	100	567.9	142.3	434	956
Hawaii	105	604.7	87.8	452	826

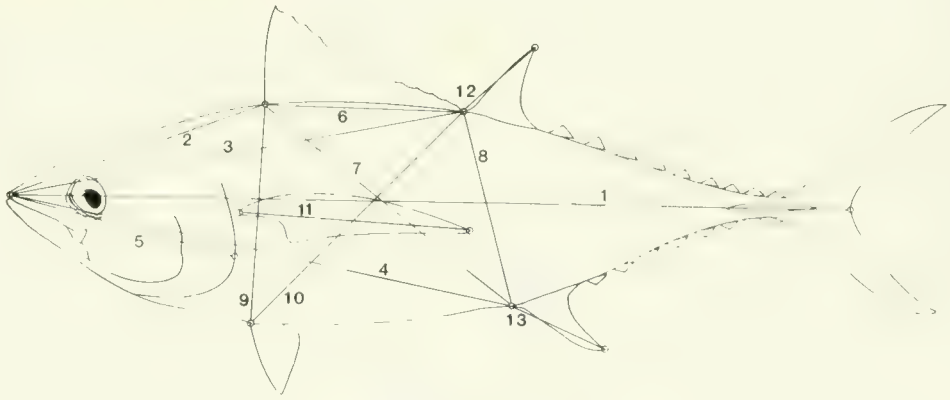
Thirteen linear measurements (Fig. 2) were made with calipers on each specimen within 24 hours of capture, and recorded to the nearest millimeter, according to methods described by Marr and Schaefer (1949). The number of gill rakers on the upper and lower limbs of the first left gill arch were also recorded for each fish. Counts for the lower limb included the single gill raker present at the angle between the upper and lower limbs (Collette and Nauen 1983). Sex was determined by examination of the gonads of the fish from Ecuador and Australia, and this subset of fish was used to test the hypothesis of no sexual dimorphism in morphometric characters of yellowfin tuna.

Statistical analyses

Because of the variation in size of fish from different areas (Table 1), morphometric data were statistically adjusted to permit comparative analysis in terms of shape independently of size (Gould 1966, Thorpe 1983).

The morphometric measurements were first transformed to common logarithms because linearity and multivariate normality are usually more closely approximated by logarithms than by the original variables (Pimentel 1979). Outliers were detected by regression analyses of morphometric characters against total length and by scatter plots of residuals versus predicted values (Cook and Weisburg 1982). When an outlier was found, all the morphometric data (but not the gill-raker data) for that fish were withdrawn from further consideration. This procedure resulted in the elimination of morphometric data for 23 fish.

Each of the morphometric characters showed a linear relationship with total length (r^2 ranged from 0.95 to 0.99), when analyzed by geographic region. Analysis of covariance (ANCOVA) was employed to test for differences in allometric relationships among samples, and to estimate the common within-group regression slopes. Within-group regression slopes were significantly different ($P<0.01$) for 10 of the morphometric characters, and thus size adjustments were based on the common within-group slopes. Coefficients from the



Acronym	Morphometric Character
TL	Total length
SFD	Snout to insertion of first dorsal fin
SSD	Snout to insertion of second dorsal fin
SAF	Snout to insertion of anal fin
HL	Head length
FDSD	Insertion of first dorsal fin to insertion of second dorsal fin
FDAF	Insertion of first dorsal fin to insertion of anal fin
SDAF	Insertion of second dorsal fin to insertion of anal fin
FDPF	Insertion of first dorsal fin to insertion of pelvic fin
SDPF	Insertion of second dorsal fin to insertion of pelvic fin
PFL	Pectoral fin length
SDFL	Second dorsal fin length
AFL	Anal fin length

Figure 2

Morphometric characters measured and acronyms used for analysis of geographic variation of Pacific yellowfin tuna.

common within-group regression are used to allometrically adjust variates when between-group heterogeneity exists (Thorpe 1976, Reist 1985 and 1986). The measurements of the morphometric characters were adjusted to those expected for the overall mean total length with a modification of the allometric formula given by Thorpe (1975):

$$\hat{Y}_i = \log_{10} Y_i - [\beta(\log_{10} X_i - \log_{10} \bar{X})]$$

where

$\hat{Y}_i$ = adjusted logarithmic character measurement of the ith specimen,

Y_i = unadjusted character measurement of the ith specimen,

β = common within-group regression coefficient of $\log_{10} Y$ against $\log_{10} X$,

X_i = total length of the ith specimen, and

$\bar{X}$ = overall mean total length.

Reist (1985) has shown that this allometric adjustment effectively removes size variation from the data he examined. This statistical approach used to remove size effects from morphometric data has been shown to be an appropriate procedure for objective analysis of the data when there is size overlap among the groups examined (Claytor and MacCrimmon 1986).

I did not adjust gill-raker counts because Spearman's rank correlation procedure indicated that there were no significant correlations between gill-raker counts and total lengths. The Kruskal-Wallis test and a nonparametric multiple comparison test (Zar 1974) were utilized to test for differences among gill-raker counts from the five areas.

I used canonical variate analysis to examine the size-adjusted morphometric data for yellowfin tuna from five locations in the Pacific Ocean. This technique, also known as multiple discriminant function analysis (Pielou 1977), is appropriate when separation of more than

two groups is desired. Canonical variates are the scores from the individual discriminant functions; that is, they are linear combinations of the original variables. The graphical display of canonical variates (for example, canonical variates 1 and 2) is useful for demonstrating differences among groups because fish that belong to the same group appear closer together on the plot than fish from different groups. Ninety-five percent confidence circles (Pimentel 1979) for group centroids can also be calculated and plotted. In addition, canonical variates can be used to examine the effectiveness of the size-adjustment procedure. Thus, canonical variates 1 and 2 were regressed against total length, and size was considered to be effectively removed if regressions were not significant (Claytor and MacCrimmon 1986).

Stepwise discriminant analysis was used to choose the combination of variables that "best" separates the groups. The resultant discriminant function was then used to classify individual fish into groups. The discriminant analysis was applied to the adjusted morphometric characters with variables entered in a forward manner using $F = 4.0$ for entering, and $F = 3.996$ for removal. The expected actual error rates of the classification function were estimated using Lachenbruch's holdout procedure (Lachenbruch and Mickey 1968, Lachenbruch 1975, Johnson and Wichern 1982). This procedure provides less biased estimates of the misclassification rate than the resubstitution method (Lachenbruch 1975). The holdout procedure, or leaving-one-out method, is based on the classification of single observations that were withheld from model development and later classified. Cohen's kappa (κ) statistic and associated 95% confidence intervals were used to determine the improvement over chance of the percent-correct classification rates (Titus et al. 1984). Given five groups, the chance of correctly classifying a single fish is 20%.

All statistical analyses were performed on a MicroVax 3500 computer. MINITAB (Ryan et al. 1976) was used to perform regression analyses and ANOVA procedures; BMDP (Dixon et al. 1981) was used to perform ANCOVA procedures and discriminant function analyses.

Results

Data from male and female yellowfin tuna were pooled in subsequent analyses because two-sample t tests for mean values of adjusted morphometric characters and gill-raker counts of fish from Ecuador and Australia indicated no significant differences between sexes (Table 2).

Total gill-raker counts and counts from the upper limb and lower limb were significantly different ($P < 0.01$) among yellowfin tuna from the five areas (Table 3). Results from the multiple comparison test for the total gill-raker-count data indicate no significant difference between the rank sums for Australia and Japan and those for Mexico and Hawaii, but these pairs are significantly different from each other and from those of Ecuador. Total gill-raker counts appeared to be a better discriminator than either the upper or lower limb counts.

The regressions for canonical variables 1 and 2 against total length (r 0.17, $P = 0.14$, and r 0.22, $P = 0.09$) were not significant, indicating that size effects had been removed from the morphometric variates. The plot of the first two canonical variates, which account for 57% and 26% of the total variation, shows complete separation of the centroid values for each

Table 2

Summary of two-sample t test for differences among male and female yellowfin tuna for 12 morphometric characters adjusted for total length, and gill-raker counts, by areas. Definitions of character acronyms are given in Figure 2. None of the t statistics are significant at $P = 0.05$.

	Ecuador			Australia		
		Mean			Mean	
Character	t	Male n 45	Female n 33	t	Male n 37	Female n 27
SFD	0.31	2.29	2.29	−1.29	2.28	2.28
SSD	0.87	2.53	2.53	0.39	2.53	2.53
SAF	0.57	2.57	2.57	0.13	2.57	2.57
HL	−1.01	2.24	2.24	−0.66	2.23	2.23
FDSD	−0.42	2.18	2.18	1.12	2.19	2.19
FDAF	0.35	2.37	2.37	0.78	2.38	2.38
SDAF	−1.04	2.18	2.19	−0.14	2.18	2.18
FDPF	−1.00	2.34	2.34	0.64	2.35	2.35
SDPF	−1.12	2.17	2.17	1.16	2.19	2.19
PFL	0.85	2.21	2.21	−0.95	2.24	2.25
SDFL	0.94	1.85	1.84	−1.52	1.91	1.92
AFL	1.07	1.83	1.83	−0.92	1.90	1.90
Gill rakers						
Upper limb	1.06	9.36	9.24	0.60	8.28	8.19
Lower limb	−0.04	21.45	21.46	−0.30	20.98	21.04
Total	−0.64	30.74	30.87	−0.81	29.27	29.48

Table 3

Gill-raker counts (means ± SD) and associated H values (Kruskal-Wallis, df 4) for yellowfin tuna from five locations in the Pacific Ocean. $^*P<0.01$.

Character	Mexico (n 101)	Ecuador (n 80)	Australia (n 66)	Japan (n 100)	Hawaii (n 100)	All (n 447)	H
Upper limb	8.4 ± 0.6	9.3 ± 0.5	8.2 ± 0.5	8.3 ± 0.6	8.4 ± 0.6	8.5 ± 0.7	127.18*
Lower limb	21.6 ± 0.8	21.5 ± 0.8	21.0 ± 0.8	21.2 ± 0.8	21.9 ± 0.7	21.5 ± 0.9	52.20*
Total	30.0 ± 1.1	30.8 ± 0.9	29.2 ± 1.0	29.5 ± 1.1	30.2 ± 1.0	30.0 ± 1.1	92.56*

group, as indicated by the 95% confidence circles for population centroids (Fig. 3). Although there is noticeable overlap of individuals, particularly of fish from Mexico and Ecuador, the fish of the eastern Pacific (Mexico and Ecuador) are fairly distinct from those of the central (Hawaii) and western Pacific (Australia and Japan). The samples from Japan and Hawaii appear to be more similar than those from Australia and Japan. The canonical variate analyses suggest that size-adjusted morphometric characters are useful for the delineation of yellowfin tuna groups. I then used stepwise discriminant function analysis to identify the most useful characters and to estimate the classification function. The stepwise analysis revealed that 11 of the 12 adjusted morphometric characters contributed significantly to the multivariate discrimination of the five groups of fish (Table 4). The approximate F statistic computed from Mahalanobis D^2 indicates a significant difference among the five groups ($F_{0.05}$ = 40.77, df 44,1585.8, $P<0.01$). The correct classification rates estimated from the holdout procedure for the 11-variable discriminant function ranged from 61.5 to 95.3%, with an overall rate of 77.6%, which is 72.0% (κ) better than would have occurred by chance (95% confidence intervals: $67.0\% \leqslant \kappa \leqslant 77.0\%$).

Pectoral fin length (PFL) is the single most useful character for distinguishing yellowfin tuna from the five groups (Fig. 4). Yellowfin tuna from Mexico and Ecuador can be distinguished from one another and from those from Australia, Japan, and Hawaii by this character alone (Newman-Keuls multiple range test). In addition to shorter PFL of fish from the eastern Pacific, the second dorsal fin length and anal fin length are shorter, relative to those of fish from Australia, Japan, and Hawaii. Head length, however, is shorter for fish from the western Pacific.

Because I was interested in improving the ability to delineate fish from Mexico and Ecuador, morphometric characters of these fish were readjusted and subjected to a second stepwise discriminant analysis. The common within-group slopes were used to adjust the morphometric characters to those expected for the overall mean total length for these two groups, employing the previous formula. The regression of the discriminant function score against total length was not significant (P = 0.37), indicating that size effects had been removed by the adjustment procedure. The frequency distribution of the canonical variable (Fig. 5) shows fairly good separation into the two groups, with only a small amount of overlap. Results of the stepwise discriminant analysis are presented in Table 5. The correct classification rate for the fish from Mexico and Ecuador was 81.3% and 88.5%, respectively, with an overall rate of 84.6%, which is 69.3% (κ) better than would have occurred by chance (95% confidence interval: $58.3\% \leqslant \kappa \leqslant 80.3\%$). Fish from the two groups were significantly different ($F_{0.05}$ = 40.00, df 6,162, $P<0.01$).

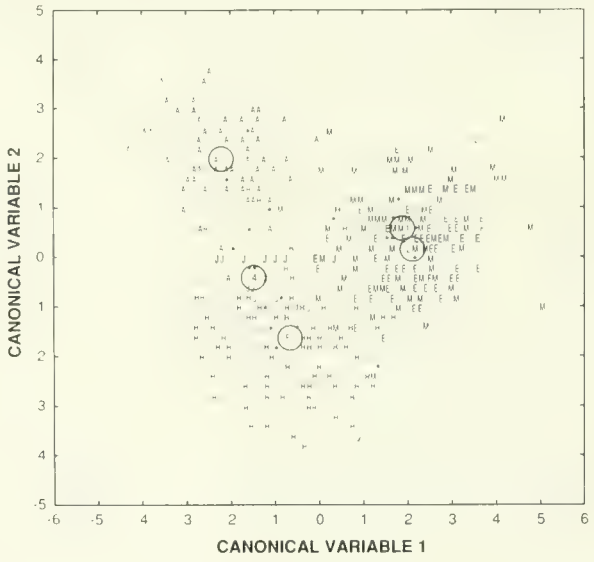


Figure 3

Plot of individuals, group centroids, and 95% confidence circles for population centroids on canonical variables 1 and 2 for the five groups of yellowfin tuna, based on 12 adjusted morphometric characters. Symbols for individual fish: M = Mexico, E = Ecuador, A = Australia, J = Japan, H = Hawaii. Overlap of individuals from different groups is indicated by asterisks. Symbols for group centroids: 1 = Mexico, 2 = Ecuador, 3 = Australia, 4 = Japan, 5 = Hawaii.

Table 4

Summary of stepwise discriminant analysis for 5 groups and 12 adjusted morphometric characters of yellowfin tuna. Character acronyms are defined in Figure 2.

Step number	Variable entered	*F* value to enter or remove	Number of variables included	Approximate *F*-statistic	Degrees of freedom	
1	PFL	154.39	1	154.39	4	424
2	SDFL	78.92	2	113.28	8	846
3	FDPF	47.73	3	92.76	12	1116.80
4	SFD	38.58	4	81.71	16	1286.81
5	HL	21.04	5	70.77	20	1393.93
6	SDPF	15.86	6	62.62	24	1462.93
7	SDAF	14.03	7	56.67	28	1508.54
8	AFL	10.24	8	51.53	32	1539.42
9	FDSD	8.09	9	47.20	36	1560.68
10	FDAF	8.01	10	43.79	40	1575.49
11	SSD	6.44	11	40.77	44	1585.82

Classification results

Group	*n*	Percent correct	Number of fish classified into group				
			Mexico	Ecuador	Australia	Japan	Hawaii
Mexico	91	75.8	69	14	2	3	3
Ecuador	78	84.6	5	66	1	4	2
Australia	64	95.3	0	0	61	3	0
Japan	96	61.5	3	0	13	59	21
Hawaii	100	78.0	3	3	4	12	78
Total	429	77.6					

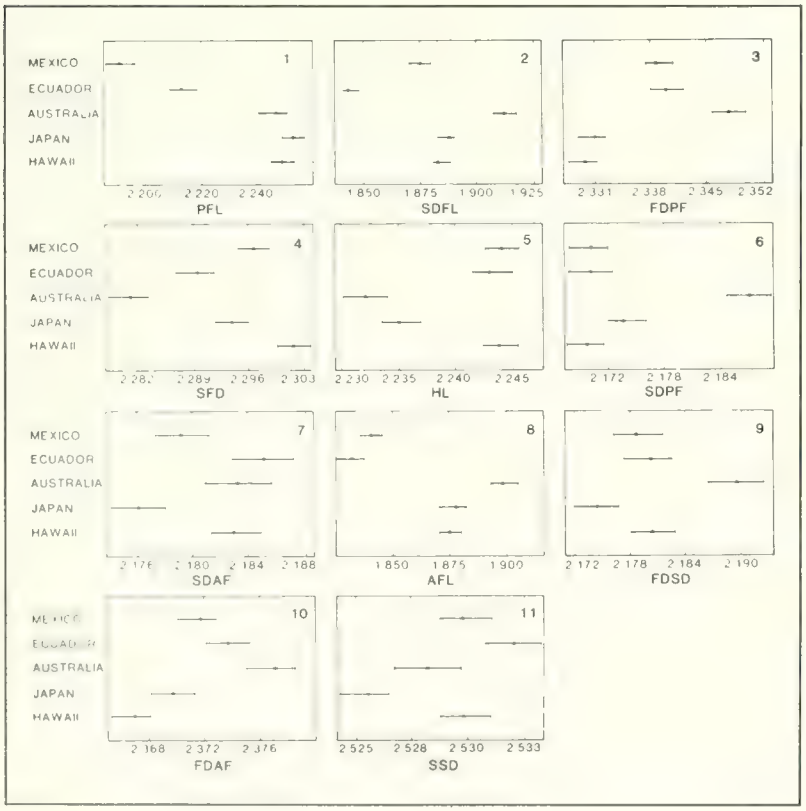


Figure 4

Means and individual 95% confidence intervals based on pooled standard deviations for morphometric characters adjusted for total length, for five yellowfin tuna sample areas in the Pacific Ocean, and the order in which they entered the stepwise discriminant analysis. Character acronyms are defined in Figure 2.

Discussion

The results of these analyses of morphometric characters and gill-raker counts suggest that each of the areas included in this investigation is inhabited by a discrete group of yellowfin tuna.

Yellowfin tuna from the eastern Pacific are morphologically more similar to one another than are fish from the central and western Pacific, as shown by the amount of overlap in the samples from Mexico and Ecuador relative to those of Australia, Japan, and Hawaii (Fig. 3). The overlap of samples from the eastern Pacific may be due to a greater degree

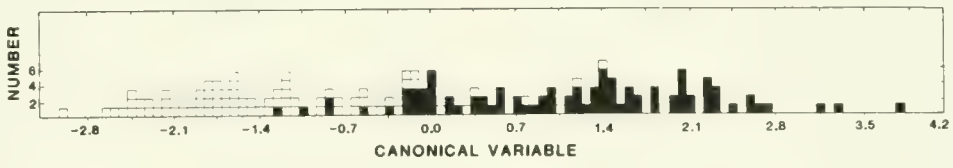


Figure 5

Frequency distribution of individual canonical scores based on 12 adjusted morphometric characters for yellowfin tuna from Mexico (open squares) and Ecuador (black squares). Centroid values for Ecuador and Mexico are −1.31 and 1.12, respectively.

Table 5

Summary of stepwise discriminant function analyses for Mexico and Ecuador groups and 12 adjusted morphometric characters of yellowfin tuna. Character acronyms are defined in Table 2.

Step number	Variable entered	*F* value to enter or remove	Number of variables	Approximate *F*-statistic	Degrees of freedom
1	SDFL	120.116	1	120.116	1 167
2	PFL	25.336	2	81.478	2 166
3	SFD	12.282	3	62.104	3 165
4	SDAF	12.988	4	53.209	4 164
5	SSD	4.730	5	44.481	5 163
6	FDSD	8.022	6	40.002	6 162

Classification results

			Number of fish classified into group	
Group	*n*	Percent correct	Mexico	Ecuador
Mexico	91	81.3	74	17
Ecuador	78	88.5	9	69
Total	169	84.6		

of mixing of the groups of fish within this region. My results agree with other studies on the morphometrics of yellowfin tuna from the Pacific Ocean: morphological differences exist among fish in the eastern, central, and western Pacific (Godsil 1948, Godsil and Greenhood 1951, Schaefer 1955, Kurogane and Hiyama 1957, Royce 1964).

One of the objectives of this study was to further evaluate the previously reported morphometric differences between northern and southern groups in the eastern Pacific (Schaefer 1989). The morphometric analysis of yellowfin tuna from the eastern Pacific by Schaefer (1989) was based upon samples from 55 locations and comprised a total of 2701 fish collected during 1974–76. Only the first eight morphometric characters shown in Figure 2 of this study were recorded and included in the analyses of that investigation. The correct classification rates from the discriminant analysis of the morphometric data from yellowfin tuna sampled from north of 15°N–20°N was 68.0%, and for those sampled from the south was 73.7%; the overall correct classification rate was 72.1%. In this study two additional morphometric characters (second dorsal and pectoral fin lengths) were selected first and second in the stepwise discriminant analysis of morphometric characters of fish from Mexico and Ecuador, indicating their discriminatory power (Table 5). The correct classification rate from the discriminant analysis for these two groups was 84.6% (Table 5). The correct classification rate from the discriminant analysis for these two groups, using the eight morphometric characters (Fig. 2) investigated by Schaefer (1989), was only 68.6%.

Total gill-raker counts of yellowfin tuna appear to be important characters which permit separation of fish from the eastern, central, and western Pacific. This meristic character also has the potential for separation of fish on a latitudinal scale as clearly indicated by the

separation of fish from Mexico and Ecuador. The gill-raker counts reported by Godsil and Byers (1944) are based upon relatively few fish from several widely scattered locations in the Pacific, but show differences between fish from Japan and those from Hawaii, Ecuador, and northern Mexico. Differences in the gill-raker counts of fish from Central America and from Hawaii have been reported by Schaefer (1955).

I recommend the use of gill-raker counts for separation on a broad geographic scale. However, this character alone is not adequate for the discrimination and classification of individuals from selected geographical locations, and should thus be collected in conjunction with morphometric data to allow finer resolution within major oceanic areas. Because 11 of the 12 adjusted morphometric characters contributed significantly to the stepwise discriminant analysis (Table 4), and because none of the 13 characters (Fig. 2) are potentially difficult to measure, I consider the set of 13 characters utilized in this study to be appropriate for future investigations of tuna morphometrics.

Extensive tagging studies designed to investigate movements of yellowfin tuna have been conducted only in the eastern Pacific (Joseph et al. 1964, Bayliff 1979, Hunter et al. 1986). Movements of yellowfin tuna in the eastern Pacific tend to be restricted, with few individuals moving more than several hundred miles. Tagging of yellowfin tuna during 1968–74 in the eastern Pacific, in inshore and offshore areas, indicated few long-distance east-west or north-south movements of the fish. The results of the present study and that of Schaefer (1989) on morphometrics of yellowfin tuna in the eastern Pacific also suggest that movements are restricted. The results of this investigation appear to be in reasonably good agreement with those of tagging studies, although several tagged yellowfin tuna released in the central Pacific have been recaptured in the eastern Pacific, and a tagged yellowfin tuna released in the western Pacific was recaptured in the eastern Pacific after traveling a net distance of 3806 miles (Peterson 1983).

Observed morphometric and meristic differences in this investigation are probably influenced both by genes and environment. It would be valuable to conduct a study of the population structure of yellowfin tuna throughout the Pacific; morphometric and meristic data should be collected, along with tissue samples to be analyzed for genetic information. Both mitochondrial DNA and nuclear genes should be screened and analyzed (Avise 1987). This approach would address the genetic basis of the groups inferred from morphometric and meristic differences. The accumulated information from morphometrics, meristics, and genetics, along with other life-history information, could then be evaluated for a better understanding of the population structure of yellowfin tuna in the Pacific Ocean.

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Abstract.–Fecundity of the yellow rock crab *Cancer anthonyi* was examined seasonally over two years. Ovigerous crabs varied in size from 89 to 153 mm carapace width. Crabs held in the laboratory brooded more than three clutches per year without molting or mating. Crab fecundity varied seasonally, with peaks in late spring–early summer and late fall–early winter. Ovigerous crabs carried an estimated 0.73–3.30 million eggs, depending on crab size, stage of egg development, and season. The log body size–log fecundity relationship changed significantly with crab embryogenesis. Estimates of reproductive potential, defined in terms of the total number of eggs produced throughout the entire adult life span, were based on the mean number of eggs produced at the mean adult size, the minimum and maximum number of mature instars, the minimum and maximum number of broods per instar, and the number of broods oviposited per year. For a female *C. anthonyi*, it was 14.7–29.4 million eggs, which was relatively higher than other members of the genus.

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Fecundity and the Reproductive Potential of the Yellow Rock Crab *Cancer anthonyi*

Jeffrey D. Shields
Department of Biological Sciences and the Marine Science Institute
University of California, Santa Barbara, California 93106
Present address: Department of Biological Sciences, Lilly Hall of Life Sciences
Purdue University, West Lafayette, Indiana 47907

Robert K. Okazaki
Department of Biological Sciences and the Marine Science Institute
University of California, Santa Barbara, California 93106
Present address: Department of Biological Sciences,
Southeastern Louisiana University, Hammond, Louisiana 70402

Armand M. Kuris
Department of Biological Sciences and the Marine Science Institute
University of California, Santa Barbara, California 93106

The yellow rock crab *Cancer anthonyi* Rathbun, 1897, supports a growing fishery in southern California. The rock crab fishery exceeds 600 tons annually ($2 million ex-vessel value), with the Santa Barbara district representing 40–60% of the total catch (Resource Agency of California 1981–87, Carroll and Winn 1988). Three species of rock crabs comprise the fishery (*C. antennarius*, *C. anthonyi*, and *C. productus*), with *Cancer anthonyi* being most prevalent in catches in southern California (Winn 1985, Carroll and Winn 1988). At present, rock crabs are exploited with no restrictions on sex or reproductive condition; ovigerous and nonovigerous females are both removed by the fishery.

Little is known about the reproductive biology of most *Cancer* species (for review, see Shields 1991). We investigated fecundity and aspects of the reproductive biology of *Cancer anthonyi* as part of a larger study that examined brood mortality resulting from nemertean predation (Shields et al. 1990). We report observations on multiple broods per crab and interbrood periods, and present an analysis of crab fecundity in relation to size, embryogenesis, and seasonality. Lastly, we define reproductive potential in terms of the maximum lifetime fecundity of an individual crab, and compare reproductive potential within the genus.

Methods

Ovigerous female crabs were trapped by a commercial fisherman at depths of 10–100 m from the Santa Barbara Channel, between Summerland and Gaviota, California (approximately 34°23′–34°25′N, 119°34′–120°12′W). Twenty to twenty-five female crabs were obtained at monthly or bimonthly intervals for two years (November 1981–November 1983). We sampled 345 ovigerous *Cancer anthonyi* of which 311 were completely processed (see Shields et al. 1990). Carapace width (CW) was measured, and the entire second left pleopod was excised and stored in 5% formalin in seawater for further analyses. Crabs were then released or maintained in flowing seawater aquaria for additional observations.

Embryogenesis was examined by observing embryos throughout the developmental process. The time to eclosion, interbrood period, and the effect of temperature on embryogenesis were examined in crabs maintained in aquaria with running seawater at normal oceanic temperatures. Crabs maintained in aquaria were fed market squid or mackerel weekly or biweekly. For statistical analyses, broods were grouped on the basis of the embryogenic development of attached eggs; i.e., embryos were in early (I–II), middle (III–IV), or late (V–VII) stages of development, or near hatching (VIII). Roman numerals refer to the developmental stages of embryogenesis (EDS) of Shields and Kuris (1988a) and Shields et al. (1990).

The term fecundity is here defined as the total number of live eggs carried by each female at any given time during incubation. Fecundity per pleopod was estimated as in Shields et al. (1990); it represents the number of live eggs on the 2d left pleopod. In addition, the actual fecundity per crab was determined for 12 crabs (96 pleopods). The fecundities of other crabs were then estimated using the regression of fecundity/pleopod with the fecundity of the 12 crabs.

Statistical analyses (ANOVA, ANCOVA, linear regression, Sidak's inequality) were conducted with the aid of SAS (1982). The log-transformation was used to reduce differences in variance between groups. A value of $P<0.05$ was accepted as significant. Data from all of the 2d left pleopods were statistically independent. Two statistics were used to minimize the influence of outliers on the analysis of covariance of log fecundity and log size between seasons, and between EDS groups. An outlier was removed from the ANCOVA and the subsequent regression analyses only if the value of its studentized residual was ± 1.50, the value of its Cooke's D influence statistic was greater than 0.006 (SAS 1982), and only if these statistics were consistent between transformed and untransformed data (5 outliers in early and middle embryogenesis). We suggest that the 5 outliers were bearing a second or third brood between molting and mating events, hence their fecundity was low (see below).

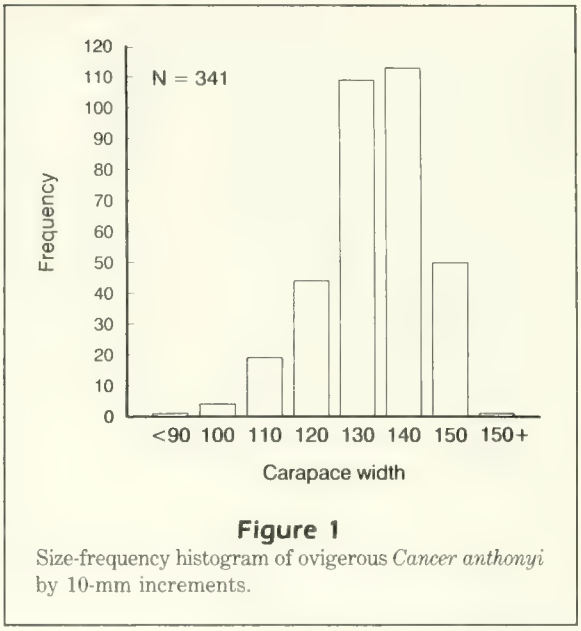

Figure 1

Size-frequency histogram of ovigerous *Cancer anthonyi* by 10-mm increments.

Table 1

Brood and interbrood period (days) for three groups of *Cancer anthonyi* females. Crabs were trapped while ovigerous, and the initial interbrood period was recorded after eclosion. All values are expressed as means (± SD); N = number of crabs. Numbers of crabs decreased within each group as a result of mortality.

Group	Brood	Days	Temp. (°C)	N	Interbrood	Days	Temp. (°C)	N
A					I	42.9 ± 20.5	14.3 ± 0.7	16
	I	40.7 ± 3.1	14.6 ± 1.1	16	II	49.4 ± 18.1	15.3 ± 1.2	12
	II	33.7 ± 4.1	16.6 ± 1.5	11				
B					I	45.9 ± 28.4	10.5 ± 1.3	15
	I	51.8 ± 4.4	10.9 ± 1.9	13	II	25.1 ± 5.2	12.6 ± 1.5	10
	II	38.2 ± 3.5	13.1 ± 1.0	12	III	48.0 ± 27.5	12.5 ± 0.7	10
	III	45.6 ± 5.8	12.4 ± 0.9	9				
C					I	26.9 ± 9.6	14.1 ± 0.7	8
	I	35.8 ± 3.8	14.9 ± 1.8	8	II	55.0 ± 30.5	15.1 ± 1.6	7
	II	34.3 ± 3.1	16.2 ± 1.6	3				
Total		40.0 ± 6.6	14.1 ± 2.1			41.9 ± 11.5	13.5 ± 1.6	
	Range (29–58)				Range (16–123)			

Results

General observations

Ovigerous females varied from 89 to 153 mm in carapace width (Fig. 1), with a mode at 140 mm. Broods of *C. anthonyi* were oviposited without observed prior mating or molting by the female crab, and were observed for every mature crab held in the laboratory; some crabs brooded at least three clutches per year in the laboratory (Table 1). At a mean seawater temperature of 15°C, crab eggs took approximately 40 days to develop from oviposition to eclosion (Table 1). Subsequent broods were typically produced within 1–2 months after eclosion of the previous brood. Crab embryos from subsequent broods (second and third) were viable and hatched normally. In addition, the seminal receptacles of 24 crabs that were dissected after the eclosion of at least a second brood contained viable spermatozoa.

Broods oviposited in sand- and gravel-bottomed aquaria were smaller than those from crabs in the field (mean fecundity/pleopod = 2.75 ± 0.73(SD) $\times 10^5$, versus 4.10 ± 0.67 (SD) $\times 10^5$; $N = 12$ and 12, respectively; $t = 4.72$, $P < 0.001$); but food or holding effects may have confounded ovarian development and fecundity in lab-held crabs.

Cancer anthonyi brooded an estimated 0.73–3.30 million eggs per clutch depending on crab size. Crab fecundity (log fecundity/pleopod) was significantly different between broods in different stages of embryogenesis (Table 2; ANOVA, Sidak's inequality, $P<0.05$). Clutch size did not differ significantly between broods in early and middle stages of development, hence these broods were combined for the size-fecundity analyses.

At eclosion, female crabs actively aided the hatching process. Females stood upon all of their legs and vigorously aerated their brood by agitating their abdomens and pleopods. Water currents through the gill chamber appeared to reverse their usual direction and flowed anteriorly through the egg mass. This facilitated eclosion, and pushed hatched prezoeae out of and away from the clutch. Within 2–3 days after hatching, female crabs stripped their pleopods of empty and dead eggs. The setae of cleaned pleopods attained a golden sheen comparable to their appearance on a freshly molted crab.

Table 2

Changes in log fecundity/pleopod with embryogenesis. EDS refers to developmental stages of embryogenesis [class 1, EDS I–II; class 2, EDS III–IV; class 3, EDS V–VII; class 4, EDS VIII] (Shields and Kuris 1988a, Shields et al. 1990). Days of development are based on temperatures of 15°C. Values with different letters are significantly different (ANOVA, Sidak's inequality, $P<0.05$).

EDS class	Days of development	N	Fecundity/pleopod (log no. of eggs) ± SD	
1	1–12	97	5.504 ± 0.200	A
2	13–30	129	5.517 ± 0.201	A
3	31–38	78	5.399 ± 0.239	B
4	39–40	31	4.748 ± 0.421	C

Size-fecundity relationship

The fecundity per pleopod (log) was positively correlated with crab size (log CW) (R 0.521, $P<0.001$, N 219; Fig. 2), but fecundity per crab (log) was not

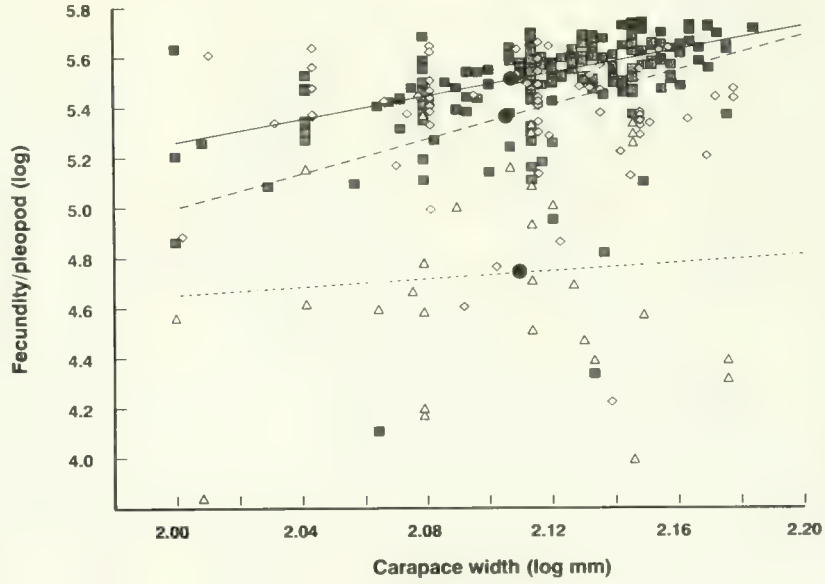

Figure 2

Size (CW)–fecundity relationships for *Cancer anthonyi* with broods in different stages of embryogenesis. Fecundities of crabs with eggs in early and middle stages of embryogenesis (boxes, solid line) and late embryogenesis (diamonds, dashed line) were highly correlated with crab size (in early and middle EDS, log fecundity/pleopod = 2.135(log CW) + 1.015, $R = 0.521$, $N = 219$; in late EDS, log fecundity/pleopod = 3.321(log CW) + 1.637, $R = 0.544$, $N = 70$; $P<0.001$ for both). Fecundities of crabs with eggs near hatching (triangles, dotted line) were not correlated with size (log fecundity/pleopod = 0.723(log CW) + 3.217, $R = 0.055$, $N = 30$, $P>0.05$). See text for ANCOVA results.

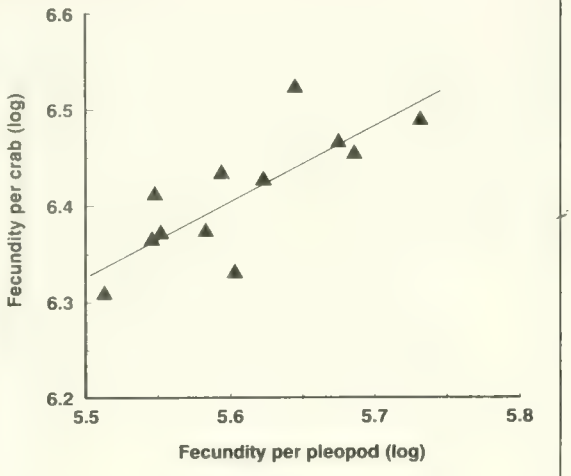

Figure 3

Relationship between fecundity per pleopod (X) and fecundity per crab (Y) for 12 crabs (log Y = 2.124 + 0.765 log X, $R = 0.782$, $N = 12$, $P<0.01$). The regression equation was used to calculate fecundity per crab for estimates of reproductive potential for *Cancer anthonyi*.

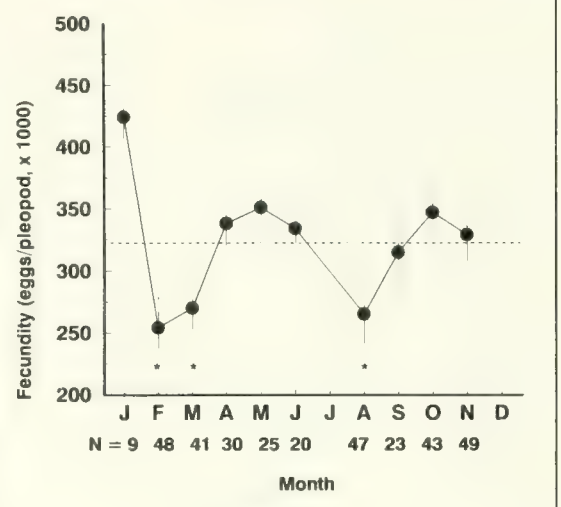

Figure 4

Seasonal variation in the fecundity per pleopod of *Cancer anthonyi*. Months with significantly less fecundity than other months are denoted with an asterisk (ANOVA, Sidak's inequality, $P<0.05$). Bars represent standard error of the mean; N = sample size; dashed line = mean fecundity.

correlated with crab size (R 0.449, $P>0.05$, N 12). The partial correlation of fecundity with crab size was significant when fecundity per pleopod was held constant (partial correlation: R 0.635, $P<0.05$, N 12). Thus, projections of reproductive potential (based on estimates of the fecundity per crab) were derived from the correlation of fecundity per pleopod with fecundity (Fig. 3).

In addition, the relationship between fecundity per pleopod and crab size was significantly influenced by embryogenesis (Fig. 2). Slopes of the regressions and adjusted mean fecundities were significantly different between EDS groups (ANCOVA, adjusted means, $F_{(2,315)} = 224.57$, $P<0.01$; separate slopes, $F = 62.71$, $P<0.01$). Fecundity was not correlated with crab size when hatching was imminent (Fig. 2).

Seasonal relationships

Crab fecundity varied seasonally (Fig. 4). Fecundity data from both years were combined for the seasonal analysis since their seasonal patterns were similar (ANOVA, log transformation, between years, within months, $P>0.05$). In February, March, and August, the mean fecundity/pleopod was lower than at other times of the year (ANOVA, log transformation, Sidak's inequality by month, $P<0.01$). The differences in mean fecundity/pleopod cannot be attributed to differences in crab size (CW) or developmental stage (EDS) during those months (two-way ANOVA with interaction, $P>0.05$, n.s.); they represent seasonal fluctuation in crab fecundity.

The size-fecundity relationship was significantly affected by seasonality. Crabs in late-winter and late-summer months (February, March, and August) brooded significantly fewer eggs than crabs of similar size in other months (ANCOVA, adjusted means of log fecundity/pleopod = 5.522 ± 0.012 (SE) versus 5.564 ± 0.006, respectively, $P<0.0025$). The slopes of the regression of log size on log fecundity/pleopod were also different between seasons (ANCOVA, separate slopes analysis, $b_{winter-summer} = 1.556$ versus $b_{spring-fall} = 2.573$, $P<0.001$). While these data show significant statistical variations, their biological significance remains speculative.

Discussion

Most *Cancer* crabs carry a single brood through a single reproductive season. While multiple ovipositions after a single mating have been reported, they generally occur in two or more reproductive seasons (Williamson 1904, Knudsen 1964, Krouse 1972, Haefner 1976, Ebert et al. 1983). Indeed, multiple ovipositions during a single reproductive season have only been reported for *C. anthonyi* (this study), *C. antennarius*

(Shields, Okazaki, and Kuris, pers. observ.), and *C. productus* (Knudsen 1964).

Ovigerous *Cancer anthonyi* occur throughout the year in southern California. The proportion of ovigerous females in the female crab population varied seasonally, with a peak in the number of ovigerous crabs in March and a nadir in the ovigerous population in June (Reilly 1987). Crab fecundity, however, followed an opposite pattern. *Cancer antennarius*, which has a geographic range similar to *C. anthonyi*, bears eggs throughout the year with a peak in reproduction during the winter months (Carroll 1982).

Ovigerous *C. anthonyi* were highly fecund. Although body size and fecundity are highly correlated in the Brachyura (Hines 1982), for *Cancer* the larger crabs *C. magister* and *C. pagurus* bear relatively fewer eggs than *C. anthonyi* (Table 4). Differences in fecundity may be partially explained by differences in egg and zoea I size, and the duration of embryogenesis (Table 3), which in turn may be explained by climatic regime (Hines 1986). While the data remain incomplete, we note two general patterns: (1) Some species of *Cancer* produce many small eggs (higher fecundity) that quickly develop into small larvae, and (2) some species produce relatively larger eggs (lower fecundity) that slowly develop into large larvae.

Decreases in fecundity per pleopod during embryogenesis are mostly a result of nemertean predation or mechanical abrasion (Shields et al. 1990). The decrease is apparently related to crab size; larger crabs appear to lose relatively fewer eggs throughout embryogenesis than do smaller crabs. The impact of nemertean predators on the fecundity of the shore crab *Hemigrapsus oregonensis*, was also greater on smaller crabs (Shields and Kuris 1988b). While smaller crabs may be more numerous in a population (e.g., Gutierrez and Zuniga

Table 3

Comparative features of embryogenesis (diapause, D), egg size (widest diameter), length of zoea I, duration of larval development (zoea I to megalopae), female size at maturity, and fecundity for ten species of *Cancer*. Unknown data are indicated (?).

Species	Embryogenic development (in days)	Egg diameter (μm)	Zoea I length* (mm)	Larval development (in days)
C. antennarius[1]	50–60	?	1.3	?
C. anthonyi[2]	29–58	265–300	1.2	33–45
C. borealis[3]	?	305	1.2	?
C. gracilis[4]	?	?	1.2	?
C. irroratus[5]	176–235 (*D*)	?	1.5	?
C. magister[6]	90–120	400–440	2.5	45–160
C. oregonensis[7]	103–118	?	?	?
C pagurus[8]	235–265 (*D*)	450–500	1.8	35+**
C productus[9]	~120	?	1.8	~95
C. setosus[10]	?	450	?	?

*Length of zoea I is carapace vertex to telson tips. Data from Ingle (1981).
**Does not include duration of megalopa stage.

References: [1]Carroll 1982, Shields et al. unpubl. data; [2]This study, Anderson and Ford 1976; [3]Haefner 1977, Carpenter 1978; [4,7,9]Knudsen 1964; [4,6,7,9]Orensanz and Gallucci 1988; [5]Shotton, 1973, Krouse 1976, Haefner 1976, Reilly and Saila 1978, Campbell and Eagle 1983; [6]Wild 1983abc, Hankin et al. 1985, Shirley et al. 1988; [8]Edwards 1979, Brown and Bennett 1980, Nichols et al. 1982, Le Foll 1986; [9]Toole 1985; [10]Gutierrez and Zuniga 1976.

Table 4

Range in size of ovigerous females, number of broods per instar, maximum number of adult instars, estimated range in fecundity per brood, and individual reproductive potential in various *Cancer* crabs. Unknown data are indicated (—), incomplete data (?), and numbers in parentheses represent the potential number of broods in later instars. For key to references, see Table 3.

Species	Size (mm CW)	Broods per instar	Max. avg. no. adult instars	Est. range in fecundity per brood	Individual reproductive potential (eggs)
C. antennarius[1]	116–143	1–2	5	$\sim 1.0 \times 10^6$	$5.0–10.0 \times 10^6$
C anthonyi[2]	90–153	2–3	3–4	$0.7–3.3 \times 10^6$	$14.7–29.4 \times 10^6$
C. borealis[3]	105–135	1 (?)	—	$0.3–1.6 \times 10^6$	—
C gracilis[4]	54–100	1 (2)	2	?	—
C. irroratus[5]	21–100	1	1–6?	$4.4–567.7 \times 10^3$	$1.7–2.1 \times 10^6$
C. magister[6]	110–170	1 (2)	3–4	$0.5–1.5 \times 10^6$	$3.0–4.0 \times 10^6$
C. oregonensis[7]	10–43	1 (2)	6	$1.0–3.3 \times 10^4$	$<0.2 \times 10^6$
C. pagurus[8]	133–205	1 (3)	3?	$0.5–3.0 \times 10^6$	$5.3–8.7 \times 10^6$
C. productus[9]	70–129	1 (2)	3	?	—
C. setosus[10]	83–151	1 (?)	2–3?	$0.6–1.7 \times 10^6$	$2.3–3.5 \times 10^6$

1976, Hankin et al. 1985), their overall contribution to the production of planktonic larvae may be relatively equal to or less than that of the less-abundant larger females whose eggs may have a greater chance of surviving embryogenesis.

Cancer anthonyi has a high reproductive potential (Table 4). Estimates of reproductive potential are typically based on the growth, size at maturity, longevity, and fecundity of an animal (Campbell and Robinson 1983). These estimates have been applied to animals having but a single brood per year. Here, we define reproductive potential for an animal capable of producing more than one brood per year (reproductive potential: mean number of eggs produced at mean adult size, minimum and maximum number of mature instars, minimum and maximum number of broods per instar, and the estimated number of broods per year). We use the **maximum** or **entire** adult life span because (1) late instar females may contribute most to the overall egg production of their cohort, (2) estimates of adult mortality are unknown for most species, and (3) confounding correlations between fecundity and mortality are eliminated (Shields 1991). While admittedly crude, the estimates of reproductive potential are useful for comparisons (Table 4). The reproductive potential of a single female *C. anthonyi* was estimated at 14.7–29.4 million eggs in her lifetime (2.6 million eggs/brood at mean size, 3–4 broods/year, 2–4 reproductive years). *Cancer magister* has an estimated potential of approximately 3–5 million eggs (1–1.5 million eggs/brood, 1 brood/year, 3 reproductive years; MacKay 1942). Neither of these estimates consider smaller broods from older instars or variations in brood size within an instar.

Most *Cancer* crabs breed but once a year, making study of their reproduction and reproductive habits logistically difficult. The high fecundity and great reproductive potential of *Cancer anthonyi*, coupled with its frequent production of eggs, may provide an excellent model for the study of reproduction in *Cancer* crabs.

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Abstract.– For fish populations in equilibrium, estimates of Z/K and L_∞ can be obtained solely from length-frequency data by using the Wetherall length-based method. Robustness of this method to departures from equilibrium conditions is examined with a population simulation model. During disequilibrium conditions following either the initiation of a fishery or a 1-year perturbation in recruitment, estimates of both parameters, especially Z/K, are severely biased. Three-year averaging of catch length-frequencies does not substantially reduce this bias. A test, based on the chi-square statistic, is proposed for detecting population disequilibrium. Provided that the sizes of length-frequency samples are sufficiently large, the test is an effective way to detect population disequilibrium and thereby avoid biased parameter estimates.

Robustness of the Wetherall Length-based Method to Population Disequilibria

David A. Somerton
Donald R. Kobayashi

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole Street, Honolulu, Hawaii 96822-2396

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Assessments of tropical fish stocks have increasingly turned to length-based methods rather than the more traditional age-based methods, because of the difficulty in ageing tropical fishes (Pauly and Morgan 1987). Although all length-based methods use length-frequency data, they are designed to measure different biological parameters and vary in their requirements for additional types of data. Wetherall et al. (1987) examined one class of length-based methods—those designed to estimate both growth and mortality parameters without the need for additional data—and developed two new estimators: a maximum likelihood estimator and a regression estimator. The second estimator, because of its simplicity, has received the most widespread use (Wetherall 1986, Arellano 1989, Polovina 1989, Rawlinson 1989).

The regression estimator of Wetherall et al. (1987), henceforth referred to simply as the Wetherall method, estimates two parameters. The first (Θ) is the ratio of the instantaneous total mortality rate (Z) to the rate constant of the von Bertalanffy growth function (K). The second (L_∞) is the asymptote of the von Bertalanffy growth function. These parameters are estimated by regressing the mean length ($\bar{l}_i$) of all fish $\geq l_{ci}$ on l_{ci}, a cutoff length ranging from the first length category that is fully selected by the fishery (L_c) to the largest length category. Estimates of Z/K and L_∞ are then calculated as $Z/K = B/(1 - B)$ and $L_\infty = A/(1 - B)$, where A is the intercept and B is the slope of the regression.

Like many other length-based methods, the Wetherall method requires the population to be in equilibrium, a condition often not fulfilled because of variations in both the environment and the fishery (Csirske et al. 1987, Ralston 1989). Although Wetherall et al. (1987) clearly have cautioned potential users that biases may result if populations are in disequilibria, the likely magnitudes of such biases have not been addressed. This has prompted us to investigate the sensitivity of the method to two common types of perturbations: (1) a rapid increase in effort during the fishing-up stage of a fishery, and (2) a fluctuation in recruitment. In this paper, we examine the temporal patterns and magnitudes of biases associated with these disequilibria and present a simple statistical test that can be used with catch length-frequencies to detect population disequilibria and help minimize the consequent potential for biased parameter estimates.

Materials and methods

The performance of the Wetherall method can be assessed by applying it to catch length-frequencies generated by a length-based population simulation model that accounts for growth, mortality, and recruitment. The model is configured to

simulate a population of opakapaka *Pristipomoides filamentosus*, a Hawaiian deepwater snapper. Mean length-at-age (L_t) is described by a von Bertalanffy growth equation:

$$L_t = L_\infty (1 - e^{-K(t - t_0)}); \quad (1)$$

where L_∞, K, and t_0 are parameters. Estimates for these parameters ($L_\infty = 66$ cm, K = 0.24/year, and $t_0 = -0.78$ year) are from Ralston and Miyamoto (1983). As a computational convenience, however, growth is considered an incremental process:

$$L_t = L_1 + \sum_{i=1}^{t-1} DL_i, \quad (2)$$

where the annual growth increment (DL_t) is expressed as a time-differenced form of Equation (1):

$$DL_t = L_{t+1} - L_t = L_\infty e^{-K(t - t_0)} (1 - e^{-K}). \quad (3)$$

Variance in length-at-age (V_t) is described by an asymptotic function of age:

$$V_t = C(1 - e^{-Dt}), \quad (4)$$

where C and D are parameters. Estimates of these parameters can be obtained by fitting this function to size and age data obtained from Ralston and Miyamoto (1983), but the predicted variance is unrealistically large. Consequently, the parameters C = 10 and D = 0.1 are chosen to best fit the predicted-to-observed length-frequency distributions. Variance in annual growth increment is described as a time-differenced form of Equation (4):

$$DV_t = V_{t+1} - V_t = C(1 - e^{-D}) e^{-Dt}. \quad (5)$$

Recruitment is assumed to occur instantaneously at age-1 and, unless experimentally manipulated, to be identical each year. The length distribution of recruits is assumed to be normal with a mean and variance defined by Equations (1) and (4), respectively. The length distribution of the surviving members of this age-class in subsequent years (y) is estimated with the recursive relationship:

$$N_{l,t+1,y+1} = \sum_{s=l_0}^{l} N_{s,t,y} e^{-(M+QF)} P(l - s|t); \quad (6)$$

where M and F are the instantaneous rates of natural and fishing mortality, Q is a size-dependent selectivity coefficient, l_0 is the smallest individual in each age group and $P(l - s|t)$ is the conditional probability of growing an amount $(l - s)$ at t years of age. The growth-increment probability function is assumed to be normal with a mean and variance computed from Equations (3) and (5). An estimate of natural mortality (M = 0.3) is obtained from Ralston (1987); estimates of fishing mortality (F = 0.3 and 0.6) are chosen somewhat arbitrarily to bracket the probable true value for opakapaka. The selectivity coefficient Q is represented by a reparameterized logistic function of length:

$$Q = \frac{1}{1 + e^{-E(l - l_{50})}}, \quad (7)$$

where E is a parameter controlling the steepness of the function, and l_{50} is a parameter controlling the length of 50% selectivity. The parameter values of E = 0.5 and $l_{50} = 45$ cm are chosen arbitrarily. The population length-distribution is calculated by summing across all age-classes, i.e.,

$$N_{l,.,y} = \sum_t N_{l,t+1,y}, \quad (8)$$

and the catch length-frequency distribution is calculated as

$$C_{l,.,y} = N_{l,.,y} \left(\frac{QF}{M + QF}\right) (1 - e^{-(M+QF)}). \quad (9)$$

The parameters Z/K and L_∞ are estimated from the simulated catch length-frequency distribution as follows. First, the length at full vulnerability (L_c) is estimated as one length interval (1 cm) larger than the rightmost mode in the catch length-frequency distribution (Polovina 1989). Second, $\bar{l}_i$, the mean length of all fish $\geq l_{ci}$, is calculated for each $l_{ci} > L_c$. Third, $\bar{l}_i$ is regressed on l_{ci} by using weighted linear regression with weights equal to the sample size (i.e., ΣC_l for $l > l_c$). Fourth, Z/K and L_∞ are then computed from the previously specified functions of the regression coefficients.

The disequilibrium experiments are conducted as follows. For the experiments examining the fishing-up phase of a fishery, the initial population length-frequency distribution is set at the equilibrium distribution in the absence of fishing. This length distribution is generated by running the model with F = 0.0 until the population is in equilibrium (i.e., until the total population size is identical on two successive iterations). Fishing mortality at each of the two specified levels is then applied instantaneously, and the simulation is run until the population is again at equilibrium. For the experiments examining the effect of perturbation dur-

ing recruitment, the initial population length-frequency distribution is set at the equilibrium distribution with a fishery producing F = 0.6. Two types of recruitment perturbations are tested: (1) a year with twice the normal recruitment, and (2) a year with a complete absence of recruitment. After each recruitment perturbation is introduced, the simulation is run until the population is again in equilibrium. Since disequilibrium bias may be only one component of the total bias of a parameter, the disequilibrium bias is isolated by expressing it as a percentage difference relative to the equilibrium value rather than the known value of a parameter.

Population equilibrium is statistically tested by comparing a catch length-frequency distribution in any one year to those from the previous two years by using a chi-square test of independence. Rationale for this type of test is that a population in equilibrium should, except for sampling variability, produce catch length-frequencies that are identically distributed over time. Significance of the chi-square test therefore indicates that the population is not in equilibrium. Performance of the chi-square test first requires the construction of 3-by-N frequency tables, where N is the number of size categories that are jointly defined over the 3-year sequence. To do this, the largest and smallest size categories in the catch containing at least five individuals in each of the three years are determined. Then for each year, all size categories less than the lower bound of the joint interval are pooled, as are all size categories greater than the upper bound. Once the table is constructed, the chi-square test can be performed according to the procedures described in Conover (1971).

The statistical power of the test is examined in a Monte Carlo experiment in which the test is applied to catch length-frequencies generated by the population simulation model. For each disequilibrium experiment, annual catch length-frequencies are subsampled, with replacement, with subsample sizes of 100, 500, 1000, and 5000 fish. At each level of subsampling, a chi-square test of independence is then performed on each 3-year sequence of subsampled length-frequencies. Subsampling and testing are replicated 100 times, and the power is estimated as the proportion of the 100 tests that is significant at the 5% level.

To determine whether disequilibrium bias could be reduced by averaging a series of catch length-frequencies over time, the Wetherall method is also applied to simulated catch length-frequencies after they have been time-averaged. First, the catch length-frequencies for each year are converted to proportions by length. Second, the time-series of catch proportions for each size interval is smoothed by using a 3-year centered running average. Third, the smoothed catch proportions at length for each year are then multiplied by the actual catch (in numbers) for that year to recover the true sample size.

In addition to disequilibrium bias, also examined are two types of bias that can influence Wetherall estimates of Z/K and L_∞ even when the population is in equilibrium. The focus of this examination is on the variation in these biases as a function of the chosen value of L_c. To do this, the model first is run until equilibrium conditions are reached. Then for each chosen value of L_c, the Wetherall method is applied to the catch length-frequency distribution, which experiences size selection by the fishery, and to the population length-frequency distribution. Type I bias in the estimates of Z/K is expressed as the percentage difference between the estimates based on catch length-frequencies and those based on population length-frequencies. Type II bias in the estimates of Z/K is expressed as the percentage difference between the estimates based on population length-frequencies and the known values of Z/K.

Results and discussion

As Wetherall et al. (1987) have cautioned, population disequilibrium indeed leads to biased estimates of Z/K and L_∞, but the temporal pattern and magnitude of this bias vary greatly with the type of equilibrium perturbation. In the fishing-up experiment, disequilibrium bias in the estimates of Z/K is initially large and negative, but later becomes positive before decaying to zero (Fig. 1a). Increasing the fishing mortality rate increases the magnitude of the positive bias and shortens the time in which the maximum positive bias is reached. The magnitude of fishing mortality, however, appears to have little effect on the magnitude of the initial negative bias. Disequilibrium bias in the estimates of L_∞ changes with time and with fishing mortality rate in a manner similar to the bias in Z/K, but the bias in L_∞ is almost always positive and considerably smaller than the bias in Z/K (Fig. 1b). In the recruitment perturbation experiment, when recruitment is doubled for 1 year, the disequilibrium bias in the estimates of Z/K is oscillatory in time and has a pronounced positive peak and a less-pronounced negative peak (Fig. 1c). When recruitment is eliminated for 1 year, the disequilibrium bias in Z/K is again oscillatory, but the positive and negative peaks occur 2 years later and the magnitude of the bias, especially that of the negative bias, is smaller. Disequilibrium bias in L_∞ varies with time in a manner similar to the bias in Z/K, but again the bias is smaller in magnitude (Fig. 1d). Thus, the following two points emerge from these simulations: (1) Biases in both parameters can be large but vary tremendously as the size structure of the

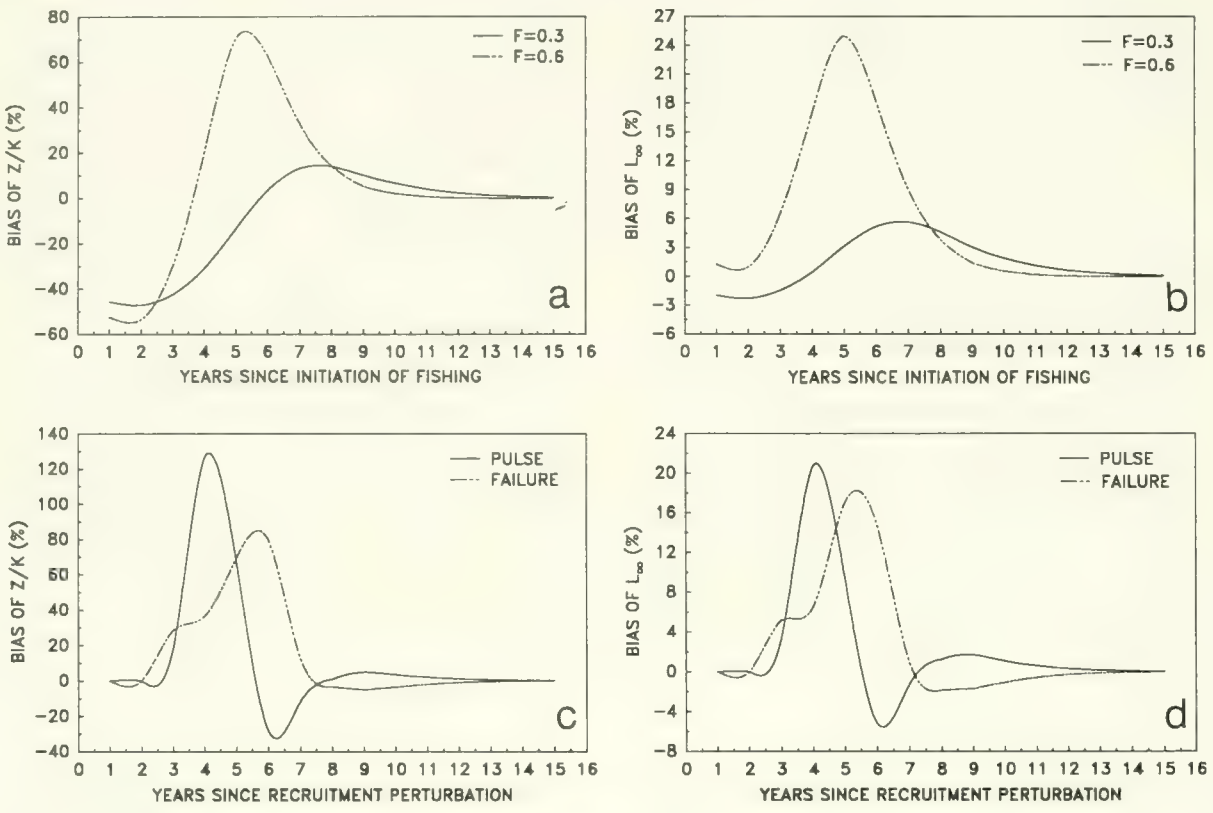

Figure 1

Temporal patterns of disequilibrium bias in the estimates of Z/K and L_∞, expressed as percentage differences relative to the equilibrium values. For the fishing-up experiment at two fishing mortality rates (F = 0.3 and 0.6), biases of (a) Z/K and (b) L_∞ are plotted against the number of years since the initiation of the fishery. For the recruitment perturbation experiment at F = 0.6, biases of (c) Z/K and (d) L_∞ are shown plotted against the number of years since a 1-year doubling of recruitment (pulse) and a 1-year absence of recruitment (failure).

population adjusts from one equilibrium to the next, and (2) bias in Z/K estimates is considerably larger than bias in L_∞ estimates.

Even though the simulated changes in fishing mortality and recruitment may be more abrupt than those typically experienced by the population, the simulations clearly demonstrate that the Wetherall estimates of Z/K and L_∞ can be quite biased when the population is not in equilibrium. As a consequence, the method apparently can be used with confidence only when population equilibrium can be demonstrated. Such a demonstration of equilibrium, or lack thereof, can be achieved by comparing successive catch length-frequencies with a chi-square test of independence. The utility of the chi-square test can best be judged by examining its statistical power to detect the disequilibrium conditions that lead to biased parameter estimates. Since the statistical power of the proposed test will increase as between-year differences in catch length-frequencies increase, it will tend to vary positively with the magnitude of parameter bias. Provided that sample sizes are sufficiently large, the test can therefore be used as a data screening device to detect when parameter bias is likely. One important consideration, then, is the relationship between sample size and the undetectable level of disequilibrium bias. This relationship can be seen by comparing the time trajectories of power (Fig. 2) with those of bias (Fig. 1).

Consider first the fishing-up experiment and bias in estimates of Z/K. For F = 0.3 and a sample size of 5000 fish, the statistical power of detecting disequilibria is high (i.e., ≥ 0.75) from years 3 to 7 (Fig. 2a). Although this interval includes most of the period in which bias is high (Fig. 1a), it does not include the first 2 years after the initiation of the fishery when bias is also high, because the proposed test requires 3 successive years of data. Furthermore, the interval of high statistical power does not include years 8–10 when bias is nearly

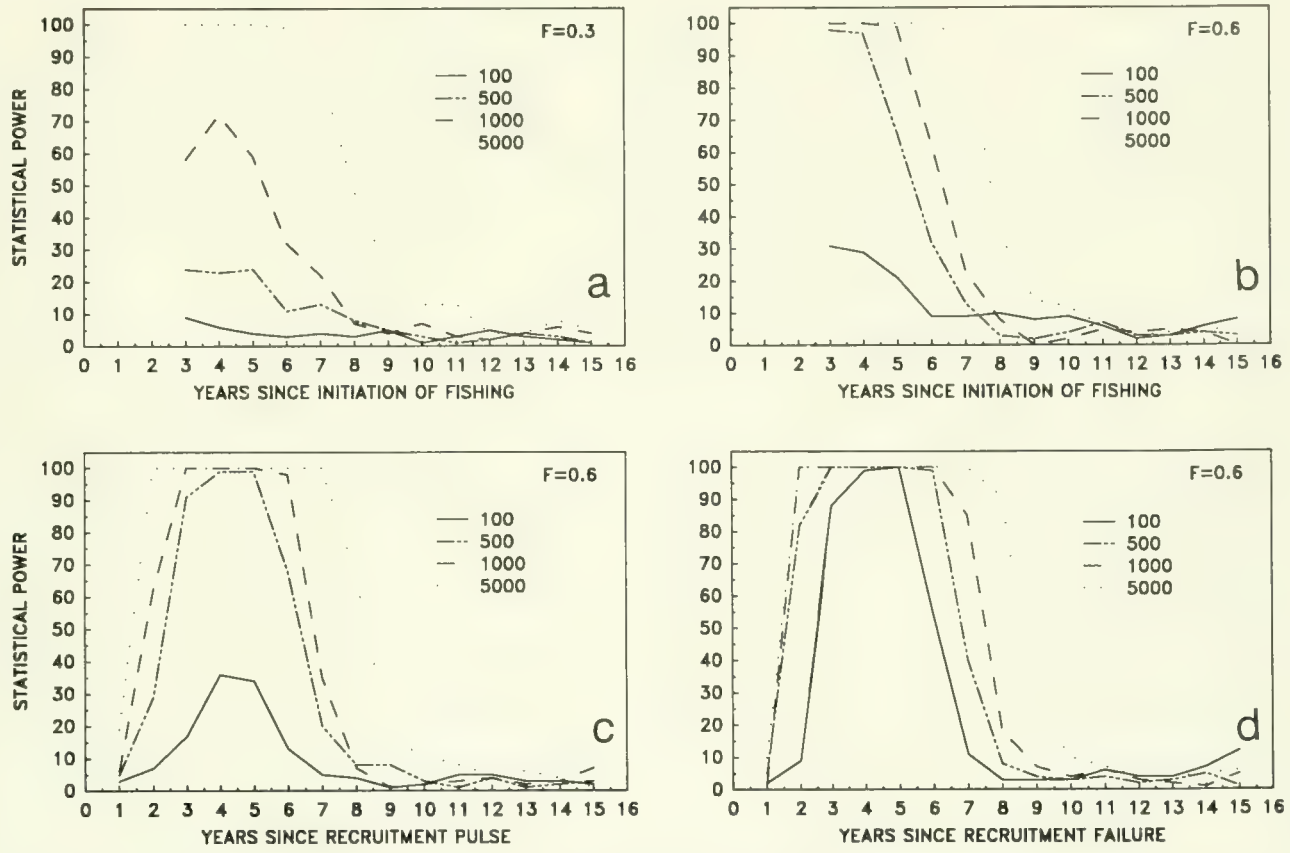

Figure 2

Temporal patterns in the statistical power of a chi-square test to detect population disequilibrium at each of four levels of sampling (N = 100, 500, 1000, and 5000). For the fishing-up experiment, power is shown for (a) F = 0.3 and (b) F = 0.6, starting in the third year after the initiation of the fishery and continuing to equilibrium. For the recruitment perturbation experiment at F = 0.6, power is shown for (c) the 1-year doubling of recruitment and (d) the 1-year absence of recruitment starting in the year in which the perturbation occurred and continuing to equilibrium.

13%. For F = 0.6 and a sample size of 5000 fish, the interval of high power is almost identical to that at F = 0.3. At lower sample sizes, however, the chi-square test is considerably more powerful when F = 0.6 than when F = 0.3.

In the recruitment perturbation experiment, statistical power is high over a broader time-interval than in the fishing-up experiment. For the case of a 1-year doubling of recruitment at a sample size of 5000 fish, power is high between years 2 and 8, an interval that includes the entire period in which disequilibrium bias is >5%. For the case of a 1-year absence of recruitment, power is high between years 2 and 8, an interval that again includes the entire period in which disequilibrium bias is >5%. Unlike the situation in the fishing-up experiments, power tends to remain relatively high with reductions in sample size. These experiments indicate that, in terms of its ability to detect the likelihood of disequilibrium bias, the chi-square test performs best on a 1-year doubling of recruitment, second best on a 1-year absence of recruitment, and worst on the fishing-up disequilibrium. The fishing-up case is worst because the test cannot be applied to the first 2 years of the time-series when bias is high and larger sample sizes are needed to detect disequilibrium.

In addition to the type of disequilibrium perturbation and size of the length-frequency sample used, the statistical power of the chi-square test also varies with the number of length-distributions included. Thus, power is calculated for tests including two, three, and four length-distributions. Since the gain in power is substantial when the number of length-distributions is increased from two to three but only minor when the number is increased from three to four, all further power simulations are based on three length-distributions.

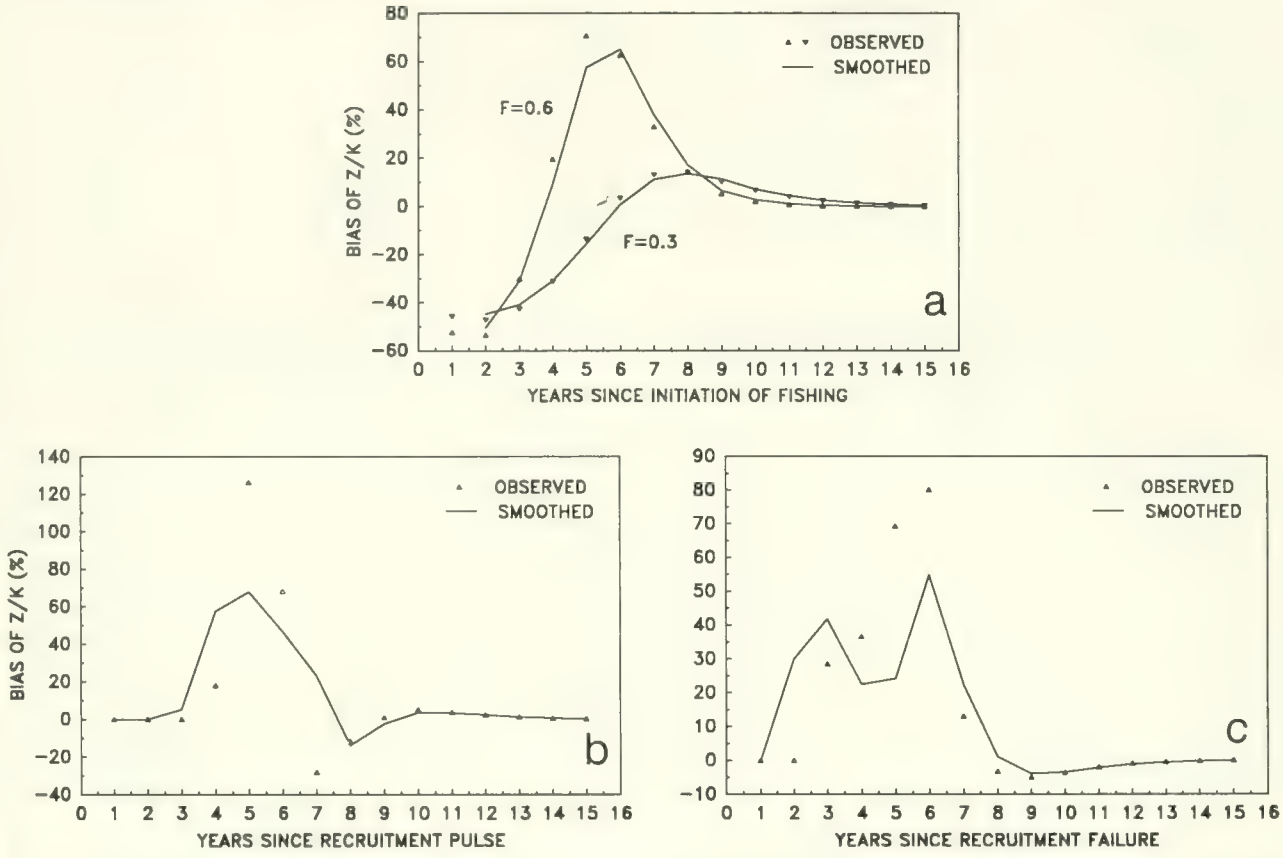

Figure 3

Effect of time-averaging catch length-frequencies, with a 3-year running average, on the bias in Z/K. (a) For the fishing-up experiment at F = 0.3 and F = 0.6, Z/K estimates based on averaged data and those based on unaveraged data are plotted against years since the initiation of the fishery. For the recruitment perturbation experiment at F = 0.6, Z/K estimates from averaged and unaveraged data are plotted against the number of years since (b) a 1-year doubling of recruitment and (c) a 1-year absence of recruitment.

If a population is found to be in disequilibrium, one can either discard the parameter estimates or find some means to reduce or eliminate the disequilibrium bias. Following the second approach, we have examined the utility of a technique often used with such age-based procedures as catch curve analysis to reduce the effects of year class variability. This technique consists of averaging the catch length frequencies over time. The effectiveness of time-averaging depends on the type of perturbation that creates the disequilibrium. In the fishing-up experiment, time averaging has essentially no effect when F = 0.3 and only a slight effect when F = 0.6 (Fig. 3a). In the recruitment variation experiment, time averaging has a somewhat greater effect, especially during the periods of maximum bias when reductions in bias are as much as 30% (Fig. 3b). Time averaging, however, also increases bias during some periods. Although time averaging is somewhat more effective when disequilibrium is due to recruitment perturbation, the 3-year time averaging employed in our study appears to be an ineffective way of reducing disequilibrium bias.

Besides disequilibrium bias, the Wetherall method is subject to two types of biases that may occur even when the population is in equilibrium. The first type of equilibrium bias (herein referred to as Type I or selection bias) is always negative and occurs when fish, equal in length to the smallest l_c values used in the regression, are not fully vulnerable to the fishery (Fig. 4a). Since, in practice, the exact form of the fishery selection curve will rarely be known, choice of the initial l_c value is somewhat arbitrarily based on the shape of a catch length-frequency histogram. Our approach follows Polovina (1989) in choosing the initial l_c to be one size-interval greater than the rightmost mode on a length-frequency histogram. This choice, however, can result in selection bias. For example, when F = 0.3, the initial l_c (51 cm) is identical to the length of 95%

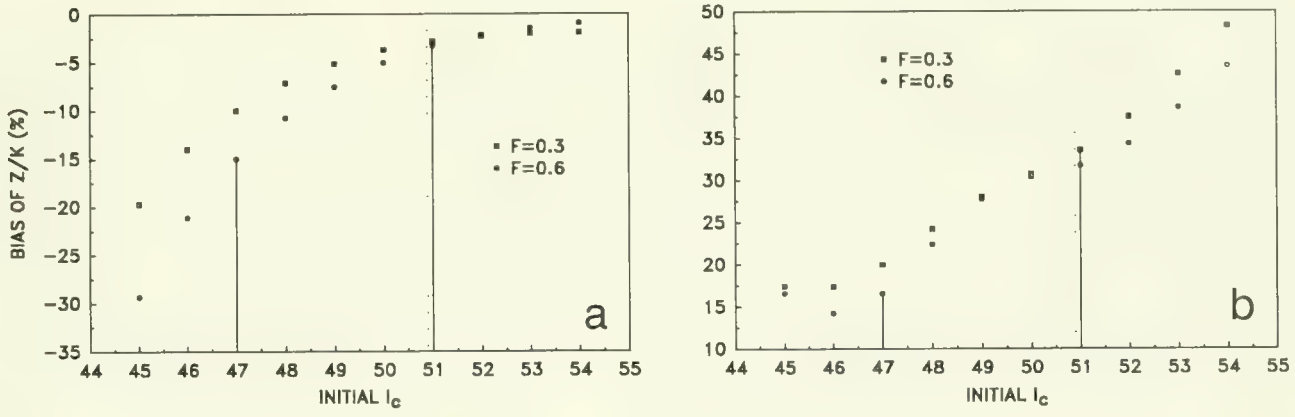

Figure 4

(a) Selection bias (i.e., bias due to inclusion in the Wetherall method of fish lengths that are incompletely selected by the fishery) and (b) residual bias (i.e., equilibrium bias that cannot be explained by selection) are shown as functions of the initial value of l_c. The l_c values (calculated as one size-interval larger than the rightmost mode in the catch length-frequency distribution) are shown as solid vertical lines at 47 cm for F = 0.6 and at 51 cm for F = 0.3. The size of 95% selection is shown with a vertical dotted line at 51 cm.

selection, and selection bias is small (3%). But when F = 0.6, the initial l_c (47 cm) is considerably less than the size at 95% selection, and selection bias is consequently larger (15%).

Since selection bias asymptotically approaches zero with increasing value of the initial l_c (Fig. 4a), one logical way of reducing equilibrium bias would be to choose a larger initial l_c. This strategy, however, would increase the second type of equilibrium bias (herein referred to as Type II or residual bias), because residual bias increases with initial l_c (Fig. 4b). For example, when F = 0.6 and the initial l_c = 47 cm, residual bias is about 16%. But when F = 0.3 and l_c = 51 cm, residual bias is 34%. Although the causes of residual bias are unknown, it could be related to either of two factors. First, as Wetherall et al. (1987) demonstrate, the estimates of Z/K and L_∞ are asymptotically unbiased as the sample size increases. Since increasing the size of the initial l_c reduces sample size, it follows that bias will increase. Second, as Laurec and Mesnil (1987) demonstrate, individual variability in growth, which has been incorporated into our simulation model, leads to bias in length-based estimates of mortality.

In the foregoing, we have demonstrated that disequilibrium bias in the Wetherall estimates of Z/K and L_∞ can be large and that time averaging does not remove such

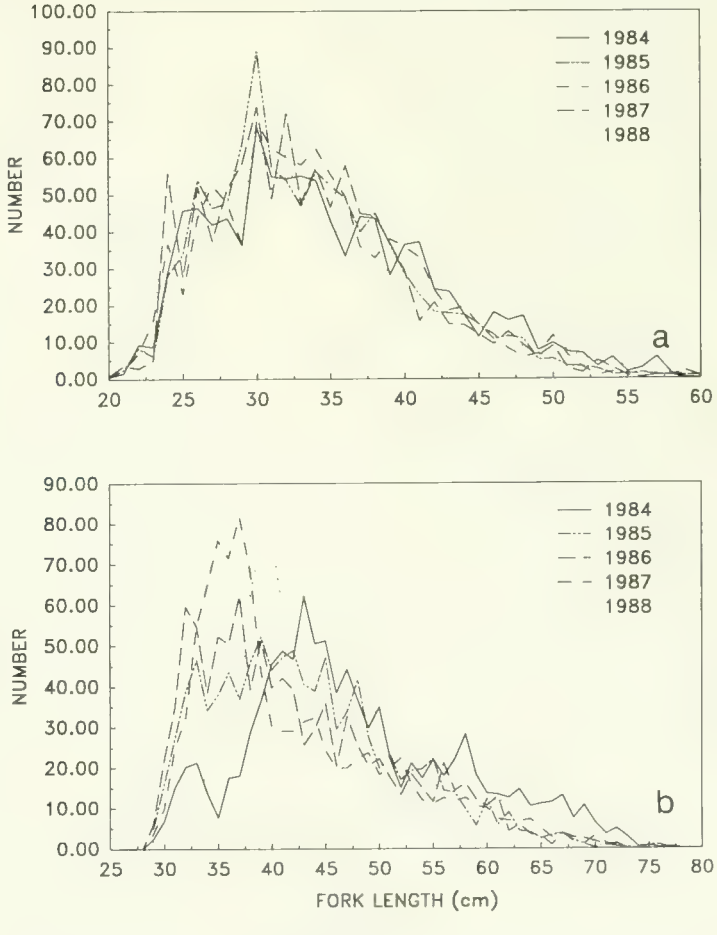

Figure 5

Catch length-frequency distributions for (a) ehu and (b) opakapaka based on 3000 fish samples collected in each year (1984–88).

bias. In light of this, the general utility of the Wetherall method clearly depends upon whether fish populations actually reach equilibrium, or conditions close enough to equilibrium, so that the consequent bias will be small. We believe, however, that equilibrium conditions may prevail more frequently than generally perceived. For example, ehu *Etelis carbunculus*, another deepwater snapper caught by Hawaii's bottomfish fishery, displays considerably less variability in size between years than opakapaka. Chi-square tests, performed on annual length-frequency samples of 3000 fish collected in 1984–88 (Fig. 5), are always not significant for ehu (1986, $P = 0.19$; 1987, $P = 0.40$; 1988, $P = 0.11$) but are always highly significant for opakapaka (1986–88, $P < 0.001$). Therefore, the ehu population is apparently close enough to equilibrium that using the Wetherall method would be appropriate. In general, however, the Wetherall method should be used with extreme caution on new or changing fisheries or species experiencing recruitment fluctuations. In all cases, its use should be preceded by a statistical verification of population equilibrium.

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Movement Patterns and Stock Affinities of King Mackerel in the Southeastern United States

Frederick C. Sutter III

Florida Marine Research Institute, Department of Natural Resources
100 Eighth Avenue SE, St. Petersburg, Florida 33701-5095

Roy O. Williams

Florida Marine Fisheries Commission, 2540 Executive Circle West
Suite 106, Tallahassee, Florida 32301

Mark F. Godcharles

National Marine Fisheries Service, NOAA
9450 Koger Boulevard, St. Petersburg, Florida 33702

Abstract.– King mackerel *Scomberomorus cavalla* were tagged and released from southeastern Florida, the Florida Keys, and South Carolina from 1975 through 1979 to document spatial and temporal movement patterns. Distance traveled by tagged king mackerel was not significantly related to size (fork length), but was correlated with number of days-at-large. King mackerel show a cyclical pattern of movement along the Atlantic seaboard of the southeastern United States and coastal waters of the Gulf of Mexico. A migratory behavior may exist in which fish return to the area of release over a period of up to 5 years. The number of fish moving away from the area of release and their direction of movement depend on whether the fish are associated with Atlantic or Gulf waters. Some king mackerel may be residents in southeastern Florida waters. The seasonal overlap between the two recognized stocks of king mackerel in southeastern Florida is estimated to be as high as 29.4–41.8%.

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Historically, the king mackerel *Scomberomorus cavalla* has supported important recreational and commercial fisheries in the southeastern United States (Finucane et al. 1986, Brusher and Palko 1987). Concern over declining king mackerel abundance has resulted in state and federal regulation of recreational and commercial king mackerel fisheries. As part of the management strategy of this resource, two migratory groups ('stocks') of king mackerel have been established for the southeastern United States (SE U.S.): an Atlantic stock and a Gulf of Mexico stock (Williams and Godcharles 1984). From 1 November through 31 March, the range for the Gulf stock includes the entire Gulf of Mexico, extending up the Florida east coast to the Volusia/Flagler county line (Fig. 1, line A). Fish found north of this line are considered to be Atlantic stock. From 1 April through 31 October, the boundary for the Gulf/Atlantic stocks is the Collier/Monroe county line on Florida's west coast (Fig. 1, line B). A 'transition' zone, therefore, is created along the southern Florida coast (Fig. 1, shaded area).

Stock definitions were largely generated from a cooperative tagging program by the Florida Department of Natural Resources (FDNR) and National Marine Fisheries Service (NMFS) to study king mackerel resources in the SE U.S. Although these data have been utilized in various resource assessments by state and federal agencies, little of this information has been formally published. In this paper, we describe the tag returns with respect to temporal and spatial movement patterns and stock affinities of *S. cavalla*.

Materials and methods

A total of 12,493 fish were tagged in four spatial/temporal regions along the SE U.S. from 1975 through 1979 (Table 1, Fig. 1). King mackerel were captured by fishermen, under contract to FDNR, using hook-and-line. Biologists from FDNR measured fork length (FL) of the fish and examined them for any debilitating injuries. Fish in good condition were placed ventral-side-up in a wet tagging cradle covered with plastic and foam rubber. A 7- to 10-mm longitudinal incision was made along the anterior portion of the abdomen permitting the insertion of an internal anchor tag with an external plastic streamer. Tagged fish were returned to the water, usually within 25–35

seconds after dehooking. Latitude, longitude, and condition of each release were recorded.

The tagging program was publicized through posters, newspaper and magazine coverage, and contacts with fishermen and fish dealers. To enhance returns, tag numbers were randomly selected for rewards of $5, $10, or $25. Recreational anglers and commercial fishermen were encouraged to provide the following information with each return: date, latitude and longitude, fork length, weight, sex, and type of recapture gear.

An accurate description of the length of each tagged and recaptured fish was needed to examine the relationship between size and movement. To determine whether particular length categories were disproportionally reported, we used chi-square tests to compare the length distributions (50 mm FL intervals) of all released fish with the length-at-tagging of recaptured fish for each of the four tagging regions. Length-at-tagging for recaptured fish was used because accuracy of recaptured-fish length measurements could not be determined and because the effects of growth prior to recapture were unknown and could bias the comparisons.

Temporal recapture relationships were determined by grouping returns into seven subareas for each of the four tagging regions along the SE U.S. (Fig. 1): South Atlantic Bight (SAB = Georgia, South Carolina, and North Carolina); northeastern Florida (NEFL = Georgia/Florida line to north side of Cape Canaveral); southeastern Florida (SEFL = north side of Cape Canaveral to Monroe/Dade line); the Florida Keys (FK = Monroe/Dade to Monroe/Collier line); southwestern Florida (SWFL = Monroe/Collier line to Apalachee Bay); the northeastern Gulf (NEG = Apalachee Bay to Mississippi River); and the northwestern Gulf (NWG = Mississippi River to Texas/Mexico border). Subareas for this analysis were chosen to provide as much resolution as possible given the distribution of tags and recaptures. Current stock

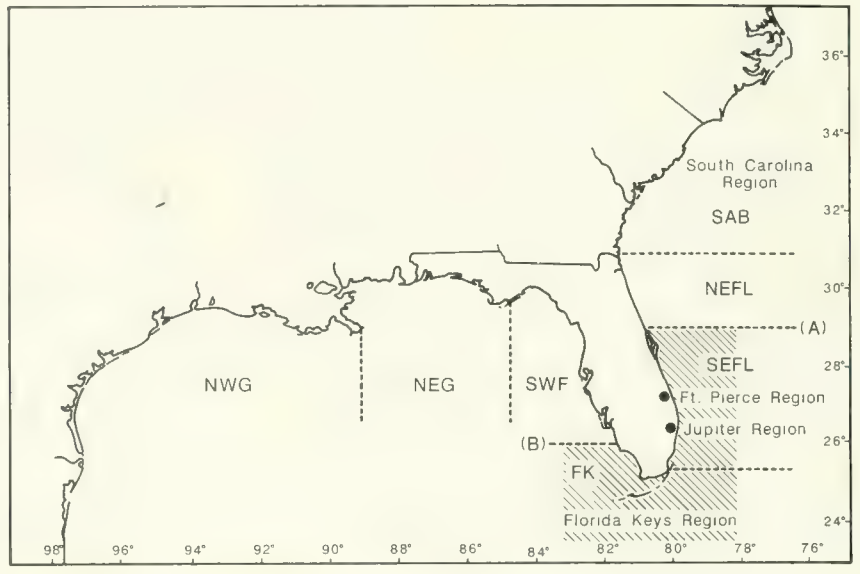

Figure 1

Location of seasonally shifting boundaries (labeled A and B) of the two stocks of king mackerel in the southeastern United States. The 'transition' zone formed by these two lines is outlined by the shaded area. Recapture subareas as defined in the text are also given (dashed lines).

Table 1

Number of king mackerel tag releases, by year.

	Location and month of release			
Year	South Carolina[1] May, June	Ft. Pierce[2] December–March	Jupiter[3] May, June	Florida Keys[4] February, March
1975	–	880	372	–
1976	–	1904	1318	974
1977	–	1666	588	844
1978	–	1966	396	776
1979	809	–	–	–
Total	809	6416	2674	2594

[1] Northern boundary of release area defined by 33°50.0′N latitude, and southern boundary by 32°03.0′N latitude.
[2] For all years, except 1975, annual totals for the Ft. Pierce area include December releases of the previous year. Northern boundary of release area defined by 28°45′N latitude and southern boundary by 27°07′N latitude.
[3] Northern boundary of release area defined by 27°07′N latitude and southern boundary by 26°19′N latitude.
[4] Eastern boundary of release area defined by 81°10′W longitude, southern boundary by 24°10′N latitude, western boundary by 83°30′W longitude, and northern boundary (Gulf of Mexico, only) by 27°00′N latitude.

definitions were considered in combination with other published king mackerel studies (e.g., Brusher and Palko 1987, Trent et al. 1987) to formulate possible subareas. The larger subareas (Fig. 1) reflect little or no tag releases and few returns, while the smaller subareas along south Florida were utilized for locations of directed tagging efforts. Returns in each subarea were sorted by year and month of recapture. A continuous time-scale, representative of the relative time of freedom and independent of actual year of release or return, was created for each subarea by designating the first 12 months after release as year 1, the second as year 2, and continuing for up to 3–5 years. Therefore, fish released in May of 1975, 1976, 1977, or 1978, for example, would be assigned a May, year-1 release date.

The spatial patterns of king mackerel returns were categorized according to the relative direction of movement through coastal SE U.S. waters rather than according to strict compass headings, because fish were released and recaptured on both the Atlantic and Gulf coasts. Fish were considered to be moving 'Atlantic-ward' if they were recaptured in Atlantic waters north of their release location or if they had moved toward the Atlantic from a release location in the Florida Keys region. Individuals were classified as moving 'Gulf-ward' if they were recaptured south of their release area or in the Gulf of Mexico. However, fish released from the Florida Keys region had to be recaptured north of the Monroe/Collier county line (B in Fig. 1) to be classified as moving Gulf-ward. Distance from tagging location was determined for each tag return. Returns were grouped into 50-km increments (i.e., 0–49km, 50–99km, etc.) when within 800km of their release site and in 100-km blocks thereafter. This created a continual distance gradient for fish moving either Gulf-ward or Atlantic-ward from each of the four tagging regions. The 100-km increments were used since only 9.5% of the recaptures occurred more than 800 km from the release sites.

The relative magnitude of movement for tagged fish moving at least 100 km away from each release location, either Gulf-ward or Atlantic-ward, was determined by plotting the cumulative percentage of fish moving through, or recaptured in, each respective distance block. A 100% value was given to the block nearest the tagging area (either Atlantic- or Gulf-ward) because all fish had to move at least 100 km to be included in the analysis. The 100-km limit was used to prevent including in the analysis fish that were exhibiting random movement patterns associated with the release locations. Since measurements of fishing effort (commercial and recreational) and catchability were not available for the time-frame of our study, we had to assume that the number of returns was a reflection of relative effort. We based this assumption on the migratory nature of this species (Beaumariage 1973, Collette and Russo 1984), knowing that fishermen target king mackerel as they become available along various coastal waters.

Stock definitions for king mackerel in the southern Atlantic and Gulf of Mexico management zones were evaluated using a discriminant function technique based on a measure of generalized squared distance (SAS 1985). The classification variable used in the analysis was membership, based on when and where a specific fish was released, of the fish in either the Atlantic or Gulf stock. Number of days at large, distance from release to recapture locations, and month and location of recapture were used as quantitative variables. A test of the homogeneity of within-covariance matrices was made to determine whether the within- or pooled-covariance matrix would be used in the discriminant function. The percentage of posterior probability of classification of each return for its original stock (i.e., Atlantic or Gulf), calculated as part of this discriminant function test, was used as an indicator of the affinity of a king mackerel for its nominal stock group. The two king mackerel stocks were then divided into five substocks to refine the indices of stock affinities. The Atlantic stock was separated into two substocks: a combination of the SAB and NEFL subareas that form the SE U.S. Atlantic coast substock; and the southern Florida summer substock, which is a conglomerate of the SEFL and FK subareas from April through October. The Gulf stock was divided into three substocks: the southeastern Florida winter substock that consists of the SEFL subarea from November through March; the Florida Keys winter substock, which corresponds to the FK subarea from November through March; and a combination of all Gulf of Mexico subareas (NEG and NWG subareas) that form the combined Gulf substock. King mackerel from a one-time tagging effort off the Texas coast during 1977 (N 319) by FDNR were included in the stock affinity analysis as part of those fish released as combined Gulf substock. These Texas fish were not included in any of the other analyses of the 12,493 tagged fish.

Results

Fish length did not influence movement and was not a factor in the probability of recapture. Neither length-at-tagging (r 0.08; df 1,147; F 0.722) nor length-at-return (r 0.075; df 1,654; F 3.688) was significantly correlated with the distance that a fish traveled from its release area. Bias associated with tag return relative to length was examined by comparing length of re-

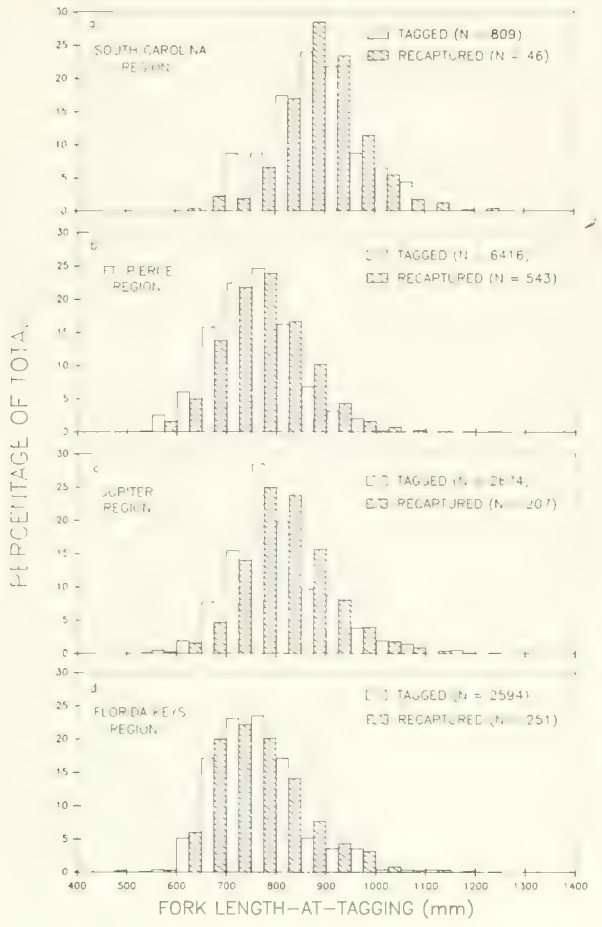

Figure 2

Length-frequencies at release and subsequent length-at-tagging of recaptured king mackerel from the four tagging regions. Fish were grouped by 50-mm FL interval; mid-range values are used for each plot.

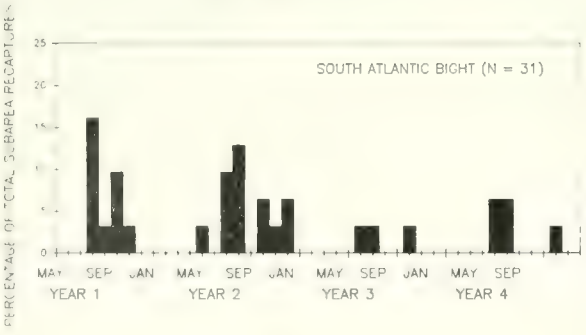

Figure 3

Monthly return percentage of king mackerel released from South Carolina region and recaptured in the South Atlantic Bight (SAB) subarea, using a continuous time-scale representative of relative time of freedom. Returns begin with May of year 1.

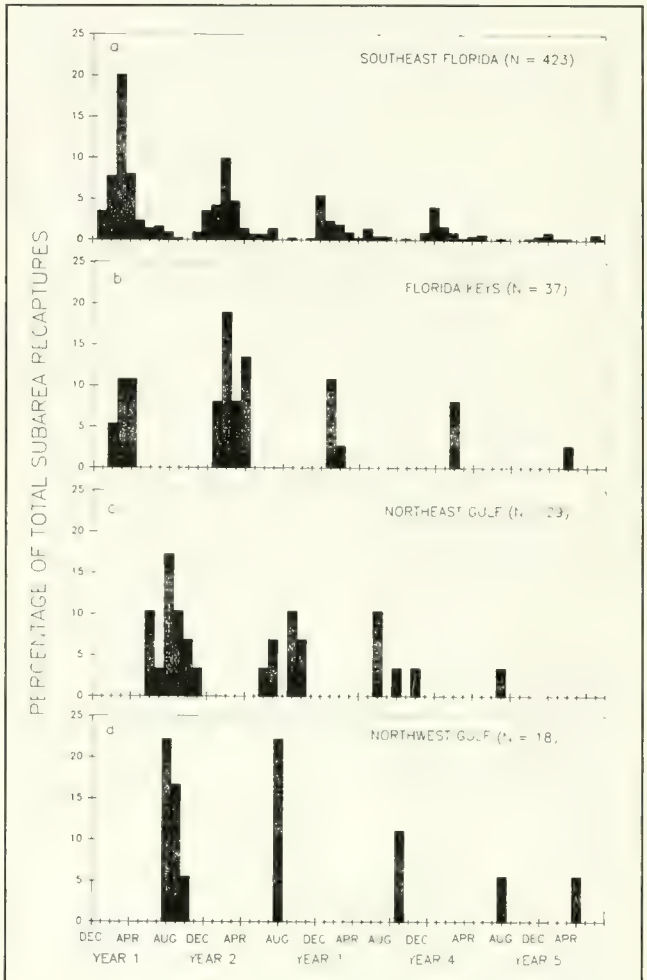

Figure 4

Monthly return percentage of king mackerel released from Ft. Pierce region and recaptured in the (a) southeastern Florida (SEFL), (b) Florida Keys (FK), (c) northeastern Gulf (NEG), and (d) northwestern Gulf (NWG) subareas, using a continuous time-scale representative of relative time of freedom. Returns begin with December of year 1.

leased fish and length-at-tagging of recaptured fish (Fig. 2a–d). No significant differences in lengths were noted for fish from any of the four tagging regions (South Carolina, χ^2 13.05, $0.25<P<0.50$, df 13; Ft. Pierce, χ^2 19.14, $0.25<P<0.50$, df 16; Jupiter, χ^2 18.76; $0.25<P<0.50$, df 16; and Florida Keys, χ^2 8.83, $0.90<P<0.95$, df 17).

Temporal recapture patterns

King mackerel released from the South Carolina region (809 tagged; 46 returned) generally returned to the SAB subarea (N 31) from June through August and from October through November of each recapture

year (Fig. 3). Insufficient returns in the other SE U.S. subareas precluded further analysis of the fish released from the South Carolina region.

King mackerel released from the Ft. Pierce region (6416 tagged; 543 returned) were recaptured in all seven subareas; numbers in four subareas were adequate to describe temporal trends (Fig. 4a–d). Peak periods of recapture in the SEFL subarea (*N* 423) occurred from December through March, with a smaller peak from May through July (Fig. 4a). The number of recaptures was highest during the first recapture year, progressively decreasing from year 2 through year 5. Fish recaptured in the FK subarea (*N* 37) from the Ft. Pierce tagging region (Fig. 4b) also showed a strong annual cycle of recapture from winter through early spring, generally following the peak recaptures from SEFL by 1–3 months. A bimodal annual cycle was noted for fish recaptured in the NEG subarea (*N* 29; Fig. 4c); the first cycle occurred during June and July, and another occurred from August through October. In NWG waters (*N* 18), returns of fish tagged in the Ft. Pierce region occurred most frequently from July through August (Fig. 4d).

The regularity of seasonal increases in tag returns from fish released in each of the Ft. Pierce region subareas indicates a predictable movement pattern. Fish move progressively through SEFL and FK waters in the late-winter and early-spring and travel to the northern Gulf of Mexico subareas during warmer spring and summer months. King mackerel then complete the cycle in late-summer and early-fall by returning to their release sites. This pattern of movement may occur over a period of 3–5 years. Whether all fish participate in this movement as part of an annual event is unknown.

Recaptures of fish released in the Jupiter region (2674 fish tagged; 207 returned) were concentrated in the SEFL and FK subareas (Fig. 5a–b). The temporal return pattern from SEFL (*N* 127; Fig. 5a) was not well defined; fish were returned in all months (most during May and June), although not in every year. The lack of a seasonal return pattern may be indicative of a year-round resident population of king mackerel in this subarea. An annual, cyclical trend for returns in the FK (*N* 25) was noted during winter months, with the magnitude of this trend decreasing over a 3-year recapture period (Fig. 5b).

King mackerel released from the Florida Keys region (2594 tagged; 251 returned) were recaptured often enough to allow a description of temporal return patterns in four subareas (Figs. 6a–d). Fish were recaptured in the SEFL subarea (*N* 34) from July through September, as well as from December through March (Fig. 6a). Recaptures in the Keys subarea (*N* 166) suggested an annual trend of returns during February and

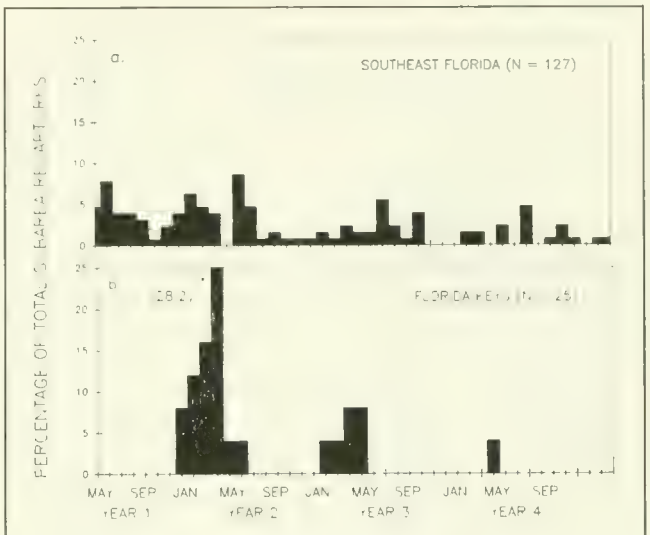

Figure 5

Monthly return percentage of king mackerel released from Jupiter region and recaptured in the (a) southeastern Florida (SEFL) and (b) Florida Keys (FK) subareas, using a continuous time-scale representative of relative time of freedom. Returns begin with May of year 1.

March, with numbers of recaptures steadily declining from Year 1 through Year 4 (Fig. 6b). A bimodal trend similar to that noted for fish released from the Ft. Pierce region (Fig. 4c) was also found for fish released from the Florida Keys region and recaptured in NEG waters (*N* 20; Fig. 6c). King mackerel returns were first reported during May and June from the NEG subarea. An increase in the frequency of tag returns from the NWG subarea (*N* 17) was then noted from June through August (Fig. 6d). King mackerel returned eastward to the NEG during August and September. These observations provide additional support for the possibility that king mackerel move annually through southeastern Florida and Gulf of Mexico waters.

Spatial patterns of movement

King mackerel exhibited different patterns in relative magnitude and directionality as they moved away from their release regions. Of fish recaptured from releases from the South Carolina region, 54.3% (*N* 25) moved more than 100km. None of these fish were reported farther north (Atlantic-ward) than North Carolina (450 km), whereas 78.6% of those moving Gulf-ward moved at least 650km to southeastern Florida waters (Fig. 7a). There was no significant difference (χ^2 0.36, $0.50<P<0.75$) in the king mackerels' direction of movement away from the South Carolina region: 44.0% (*N* 11) moved Atlantic-ward and 56.0% (*N* 14) moved Gulf-ward.

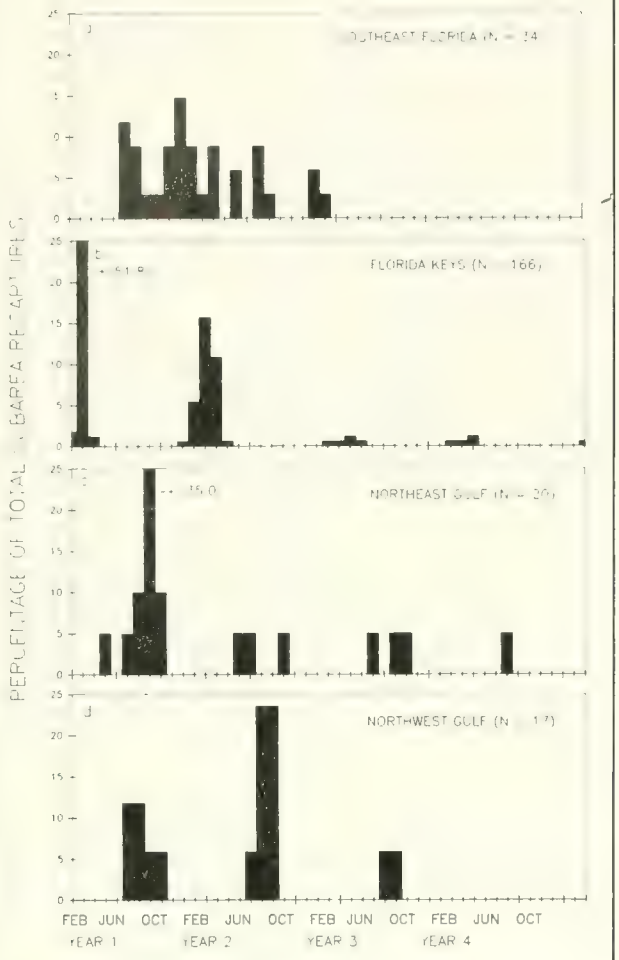

Figure 6

Monthly return percentage of king mackerel released from Florida Keys region and recaptured in the (a) southeastern Florida (SEFL), (b) Florida Keys (FK), (c) northeastern Gulf (NEG), and (d) northwestern Gulf (NWG) subareas, using a continuous time-scale representative of relative time of freedom. Returns begin with February of year 1.

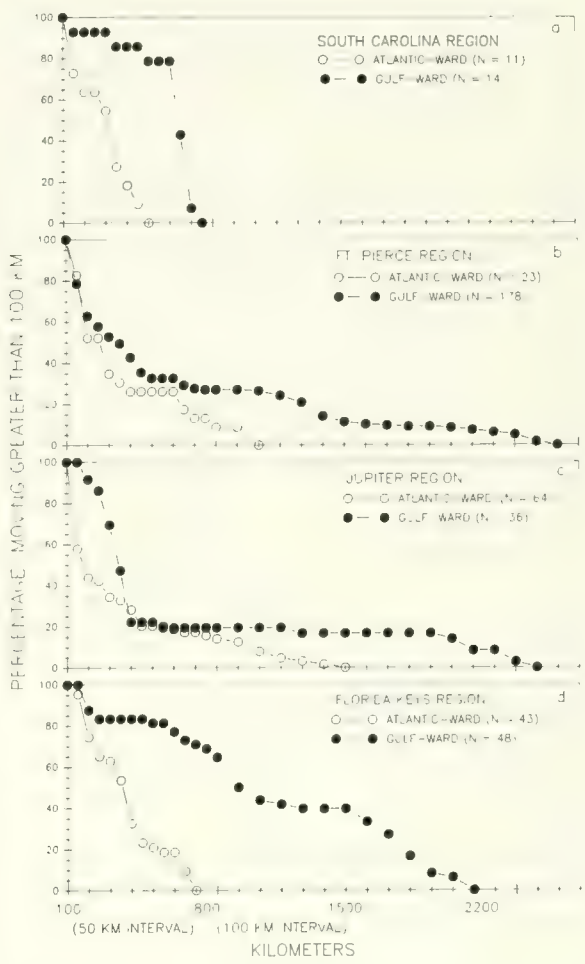

Figure 7

Relative movement of tagged king mackerel away from the four tagging regions of (a) South Carolina, (b) Ft. Pierce, (c) Jupiter, and (d) the Florida Keys, as a percentage of fish moving at least 100 km. The direction component is given by Atlantic-ward or Gulf-ward movement (see text for definitions).

A total of 37.0% (N 201) of the king mackerel recaptured from fish released from the Ft. Pierce region moved more than 100 km, with fish recaptured as far as 1000 km Atlantic-ward off North Carolina (Fig. 7b); fish moving Gulf-ward were recaptured as far away as Texas and Mexico (up to 2400 km). Within 800 km of the release site, the relative magnitude of movement away from the Ft. Pierce release region was similar for king mackerel with Gulf-ward affinity and those with Atlantic-ward affinity; however, a significantly greater number of fish (χ^2 119.53, $P<0.005$) moved Gulf-ward (88.6%; N 178). A similar trend in the relative magnitude of movement was noted for fish released from the Jupiter region; 48.3% (N 100) moved more than 100 km. A significantly higher percentage of these fish (χ^2 7.84, $P<0.01$) moved Atlantic-ward (64.0%; N 64; Fig. 7c). For fish moving more than 100 km (N 91), those tagged in the Florida Keys region moved farther from their release site into Gulf waters than did those fish moving Atlantic-ward (Fig. 7d). However, king mackerel released in the Florida Keys region did not show a significant difference in their relative direction of movement (χ^2 0.27, $0.50<P<0.75$): 47.3% (N 43) moved Atlantic-ward, 52.7% (N 48) moved Gulf-ward.

The number of days-at-large was significantly related to the distance that a fish traveled after release (Y-intercept 130.609, slope 0.072, r 0.122, df 1, 1148,

F 17.382). Several fish moved remarkable distances over short periods of time. For example, one fish released from Jupiter, Florida, traveled 2250km in 77 days before being recaptured off the southern Texas coast.

King mackerel stocks in the southeastern United States

The percentages of king mackerel released as either Atlantic or Gulf stock and classified (using the posterior probability of the discriminant function analysis) into the same stock based on time and place of recapture are given in Table 2. The chi-square value for the test of homogeneity of the within-group covariance was significant (χ^2 41.89, df 6); therefore, the within-covariance matrices were used in this analysis. A total of 66.81% of king mackerel released as Atlantic stock was classified as the same stock upon recapture; therefore, this group was given a 66.81% affinity index value (Table 2). A 76.07% affinity index value was found for the Gulf of Mexico king mackerel stock. The percentage of classification for recaptured king mackerel in the five substocks is given in Table 3, again using the within-covariance matrices in the discriminant function (χ^2 245.87, df 24). All fish released in the SE U.S. Atlantic coast substock area were recaptured within the temporal and spatial definition of the Atlantic stock; i.e., they were all classified with either the SE U.S. Atlantic coast or southern Florida summer substocks (Table 3). Therefore, the SE U.S. Atlantic coast substock was given a 100% affinity value for the Atlantic stock. Southern Florida summer substock returns were similarly examined; 4.23% were classified with the SE U.S. Atlantic coast substock, and 53.97% were classified with the southern Florida summer substock, which yielded a 58.20% affinity index value. The combined Gulf substock had a 100% affinity-index value for the Gulf stock based on returns from the Florida Keys winter substock (9.09%) and from the Gulf waters (90.91%). The affinity-index value of the Florida Keys winter substock was 90.00% (Table 3), although some fish released in this area were classified in each of the five substock areas. King mackerel

Table 2

Posterior probability values for membership in either the Gulf or Atlantic stocks of king mackerel. Numbers of recaptured fish in parentheses.

	Percentage classified into stock		
Stock	Atlantic	Gulf	Affinity index
Atlantic	66.81 (151)	33.19 (75)	66.81
Gulf	23.93 (162)	76.07 (515)	76.07

Table 3

Posterior probability values for membership in the five substocks of king mackerel. Numbers of recaptured fish in parentheses.

	Percentage classified into stock					
	Atlantic		Gulf			Affinity
Substock	SE U.S. Atlantic coast	South Florida, summer	Southeast Florida, winter	Florida Keys, winter	Gulf combined	of index
Atlantic						
SE U.S. Atlantic coast	91.89 (34)	8.11 (3)	0.00 (0)	0.00 (0)	0.00 (0)	100.00
South Florida, summer	4.23 (8)	53.97 (102)	10.58 (20)	31.22 (59)	0.00 (0)	58.20
Gulf						
Southeast Florida, winter	5.58 (26)	23.82 (111)	14.81 (69)	55.36 (258)	0.43 (2)	70.60
Florida Keys, winter	2.00 (4)	8.00 (16)	5.50 (11)	80.50 (161)	4.00 (8)	90.00
Gulf combined	0.00 (0)	0.00 (0)	0.00 (0)	9.09 (1)	90.91 (10)	100.00

released as southeastern Florida winter substock were also classified into all substocks, yielding a 70.60% affinity-index value (combined Gulf, 0.43%; Florida Keys winter, 55.36%; and southeastern Florida winter, 14.81%).

Discussion

Two movement patterns were identified from our tagging study. King mackerel released in association with the Gulf of Mexico waters were found during winter months along the Florida Keys and along the southeastern Florida coast as far north as Cape Canaveral. By spring, these fish traveled along the western Florida coast toward northeastern Gulf waters, continuing westward during the summer. These king mackerel returned toward northwestern Florida in late-summer and early-fall, and then headed back to southern Florida waters by winter. Based on the recapture of fish from the same locations during roughly the same times of year over several consecutive years (e.g., Fig. 4a–d), we conclude that a periodic (annual) migratory behavior exists. The regularity of king mackerel movements through Gulf of Mexico waters was also noted during other tagging studies (Sutherland and Fable 1980, Fable 1988).

Trends of the catch-per-unit-effort (CPUE) for king mackerel from charterboat catches, reported by Trent et al. (1987), also support our conclusions. During 1983, 1984, and 1985, CPUE values of king mackerel generally increased along the northern Florida coast during late-May and June, followed by a peak in CPUE along the Alabama, Mississippi, and Texas coastlines. Another increase in CPUE was noted in Alabama during late-July and August, followed by a peak in northwestern Florida during late-August or early-September. Only winter peaks were noted in southern Florida, whereas no CPUE pattern was established for southeastern Florida. The lack of a consistent peak in this region as determined by tag returns from southeastern Florida may be evidence for a resident (i.e., nonmigratory) population. Fable et al. (1987) noted winter resident population of large king mackerel (>800 mm FL) in the northwestern Gulf of Mexico. We found no size-component associated with tagged fish either staying or leaving southeastern Florida waters (χ^2 8.19, $P>0.975$, df 18), based on length-frequency distributions of recaptured fish (50-mm FL interval, 400–1300 mm).

Movement of king mackerel along the Atlantic coast was not as clearly defined. Fish traveled south from South Carolina waters during the spring and summer, distributing themselves along the south Atlantic coast as far as the eastern and southwestern coasts of southern Florida, and then returned northward in late-summer and early-fall. Trent et al. (1987) noted an increase in CPUE from charterboat catches from North Carolina during April and again during October and November. Progressive increases in CPUE were noted in South Carolina during May and later during August and September; peaks were noted in Georgia and northeastern Florida during late-May (after South Carolina peaks) and again during August (before South Carolina peaks).

Spring and summer movements of king mackerel may reflect migrations to their respective spawning areas. After spawning, they return to wintering areas in the fall. Ichthyoplankton collections indicate that king mackerel from the Atlantic coast spawn from April through October, with a peak during September (Collins and Stender 1987). Gulf of Mexico larvae collections and reproduction indices suggest a similar spawning season for the Gulf stock (Wollam 1970, Dwinell and Futch 1973, McEachran et al. 1980, Finucane et al. 1986).

King mackerel movement patterns, as determined from temporal and spatial variability in tag returns, must be viewed in relative and descriptive terms rather than in absolute rates of movement. The percentages of returns varied from 5.69% (South Carolina region) to 9.68% (Florida Keys region), but when numbers of recaptures were compartmentalized by subareas, these values were subsequently reduced. This reduction was magnified as distance from release site increased. Lower percentage of returns may be a function of actual proportion of fish moving away from location of release but may also reflect relative changes in effort and availability over time, or may be indicative of a "dilution" of tagged fish by king mackerel from other locations (e.g., with a resident population in the northwestern Gulf of Mexico). Combinations of these factors, as well as other environmental and biological parameters, are probably interacting, but are beyond the resolution ability of our database. However, we feel the observed trends, together with published information previously discussed, are strong enough to support our conclusions of king mackerel movement through SE U.S. waters.

Distance from the 'transition zone' along the southern Florida coast (Fig. 1, shaded area) was related to the affinity-index values calculated for each substock. Both the South Atlantic and combined Gulf substocks, located outside this transition area, had 100% classification (affinity) values with the appropriate Atlantic or Gulf stock. The Florida Keys winter substock, located in the southwest edge of this transition area, was closely tied to the Gulf stock (90.00% affinity). King mackerel released in southeastern Florida had the lowest affinity values (Table 3). Winter releases from

the Ft. Pierce region (southeastern Florida winter substock), which would be included within the scope of the Gulf stock, were mistakenly classified 29.40% of the time with Atlantic stock waters. Most of these misclassifications were temporal in nature, the recaptures having been taken during summer months from southeastern Florida. The low affinity-index value for summer-month releases from Jupiter (southern Florida summer substock) is a result of fish being recaptured within either the Florida Keys winter substock (31.22%) or the southeastern Florida winter substock (10.58%) areas, yielding a total misclassification of 41.80% of Atlantic stock with Gulf stock waters.

Southeastern Florida waters are important to both Atlantic and Gulf stocks. Both stocks occupy this area during some part of the year; the observed seasonal overlap may range from 29.40% to 41.80% (Table 3) based on percent misclassification. The management problems of a mixed-stock fishery system are recognized (Hilborn 1985, Sinclair et al. 1985). For effective management an accurate distinction between stocks is vital (Misra 1985), yet genetic differentiation using electrophoretic variation has not yielded any differences between Gulf and Atlantic stocks of king mackerel (May 1983, Johnson 1988). An alternative management strategy, therefore, may be to designate the area between the Collier/Monroe line on the southwestern Florida coast and the Florida/Georgia line on the Atlantic coast as a mixing zone, to be managed with the most conservative measures available (i.e., Gulf or Atlantic stock) to ensure adequate stock protection.

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Effect of Tag Anchor Location on Retention/Survival through Molt in Male Snow Crabs *Chionoecetes opilio*

David M. Taylor
John M. Hoenig

Science Branch, Department of Fisheries and Oceans
P.O. Box 5667, St. John's, Newfoundland A1C 5X1, Canada

Abstract.—A laboratory study showed that when small male snow crabs are tagged with the anchor of a t-bar tag inserted into the dorsal musculature, tag retention and survival through the first molt are excellent; when the tag anchor is situated in the basal leg musculature, animals die while molting. When recaptures were obtained from larger, field-tagged animals, it was noted that some animals which had molted had been tagged in the leg musculature. Dissections were performed on 43 animals which molted and 89 animals which did not molt to determine tag anchor placement. Four general locations were noted: dorsal musculature, basal leg musculature, loose in the body cavity, and attached internally to carapace. Relative tag retention/survival associated with molting was estimated for the different tag anchor locations by comparing the proportions of tags in each location among animals which molted and among those which did not. Animals with anchors in the leg musculature appeared to survive and retain the tag through a molt as well as those tagged in the dorsal musculature and those with the tag attached to the inside of the carapace. Animals with anchors loose in the body cavity appeared to have worse tag retention/survival than those tagged in the dorsal musculature. The hypothesis that tag placement does not affect retention/survival through molt was tested by fitting hierarchical loglinear models and testing for a significant interaction between molt status (i.e., did or did not molt) and tag anchor location. No statistically significant effect was found, but it still seems prudent to try to place tag anchors into the dorsal musculature.

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A tagging study was initiated in Conception Bay, Newfoundland, Canada, to determine the growth in size of male snow crabs *Chionoecetes opilio* at the time of molting. The t-bar tag (Floy Tag Mfg. Co., Inc., Seattle, WA 98105) was selected because preliminary studies had shown that the tag can be retained through a molt (McBride 1982, Taylor 1982). Early tag return rates were lower than expected, so a study was initiated to evaluate the performance of the tag when applied to animals held in captivity (Hurley et al. 1990). The laboratory study, conducted on animals ranging in size from 60 to 83 mm CW (carapace width), demonstrated that survival and retention of tags through a molt was excellent, provided the tag anchor was inserted into the dorsal musculature (Fig. 1). However, when the tag anchor was inserted into the basal leg musculature, the animals died during the molt. Tissue necrosis associated with *Pseudomonas* sp. bacteria was frequently noted around the tag anchor regardless of where it was located in the body.

For the Conception Bay study, an effort was made to carefully insert the tag anchors into the dorsal musculature. It was therefore surprising when some animals that had molted were recaptured with the anchor in the basal leg musculature. Also, some crabs had tags with the anchor loose in the body cavity, while in others it was attached to the carapace. Since the animals examined in the field study were larger (82–120 mm CW at tagging) than the ones used in the laboratory study, it was hypothesized that placement of the tag anchor may not be as critical for large animals as for smaller ones.

In this paper, we present the results of dissecting 132 recaptured animals to determine location of the tag anchor within the body. We develop analytical procedures to estimate the relative rate of tag retention and survival at the time of molting for different anchor locations. We test the hypothesis that retention/survival is the same for all locations using hierarchical loglinear models.

Materials and methods

Male snow crabs were tagged in Conception Bay during 1983 and 1984 using methods described by Hurley et al. (1990) and Taylor and Hoenig (1990). The t-bar tag consists of a vinyl anchor 8 mm long, 1.2 mm in diameter, attached perpendicularly to a 25 mm-long shaft, 0.5 mm in diameter, which in turn connects to a 50-mm length of Number 20 vinyl tubing printed with identificaion information. Tags were inserted through the posterior ecdysial suture (epimeral line) which was made visible by applying gentle upward pressure to the carapace. The location of tag insertion was on the right side of the body 2–6 mm from the coxopodite of the last walking leg (Fig. 1). Before releasing the crab, the end of the tag

was given a gentle tug. If the tag appeared loose, it was removed and the animal was discarded.

Recaptured animals were obtained from commercial fishermen and stored in a freezer. Animals were then thawed and dissected in order to determine the location within the animals of the tag anchor. The carapace was cut diagonally on either side of the protruding tag by inserting the lower blade of a pair of scissors into the epimeral line. The forward portion of the triangular piece of cut carapace was then lifted to uncover the end of the tag. Tags were classified as being in one of four positions (Table 1): (1) anchor lodged in the dorsal musculature; (2) anchor loose in the body cavity, e.g, nestled against the hepatopancreas; (3) anchor lodged in the soft, newly forming carapace under the hard carapace, or attached to the underside of the hard carapace; and (4) anchor lodged in the basal leg musculature. The extent of any necrotic tissue around the anchor was also noted (Table 2).

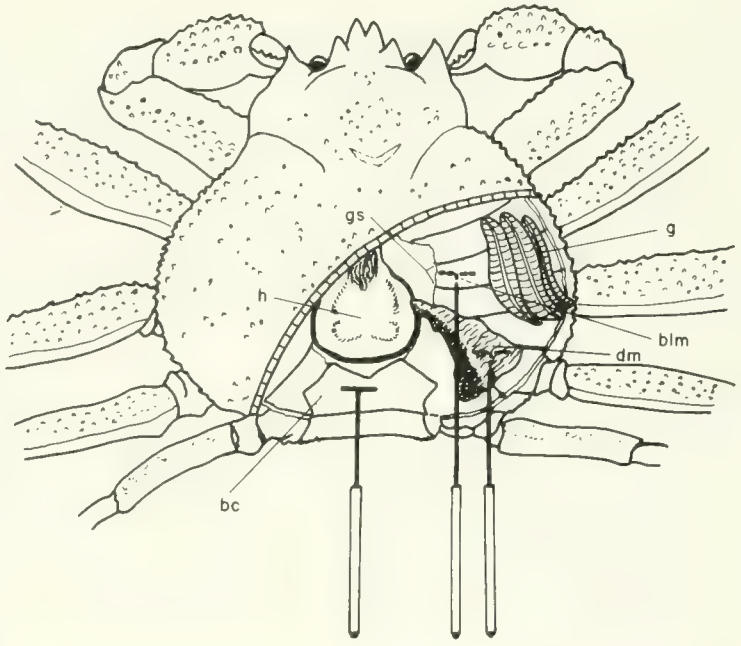

Figure 1
Drawing of a male snow crab with part of the dorsal carapace removed to show tagging locations referred to in text: bc = body cavity, blm = basal leg musculature, dm = dorsal musculature, g = gills, gs = gill septum, h = heart.

Analysis of recapture data

The logic of our analysis is as follows. We don't know the proportion of animals with the tag anchor placed in each of the four locations, and we don't know the magnitude of any initial tag loss or mortality immediately (within one month) following release of the tagged animals. However, those recaptured animals at liberty for more than one month which did not molt provide an estimate of the proportions of animals with tag anchors in each location prior to molting. Similarly, the recaptured animals which did molt provide an estimate of the proportions after molting. Consequently, differences in the proportions reflect different tag retention and/or survival.

Table 1
Recapture data for male *Chionoecetes opilio* tagged in Conception Bay, Newfoundland, given by year of tagging, molt status (molted vs. did not molt), location of tag anchor within the body, and data pooled over the 2-year period.

Recapture of animals tagged in:	Molt status	Tag locations: dorsal musculature	loose in body	in shell	leg musculature
1983	did not molt	7	2	8	7
	molted	4	1	4	3
1984	did not molt	29	14	11	11
	molted	16	1	6	8
Years combined	did not molt	36	16	19	18
	molted	20	2	10	11

This analysis requires two assumptions: (1) tags in all of the tagging locations affect the timing of molting in the same way (if at all); (2) differential mortality and tag loss among tagging locations is zero both prior to and subsequent to molting (with the possible exception of the period immediately after tagging and release of animals). A number of studies have shown that molting can be a critical period for tag-induced mortality and tag shedding (Restrepo and Hoenig 1988, Hurley et al. 1990). Hence, it is reasonable to presume that if animals survive the first month at liberty with their tag intact, then they are likely to remain viable until the time of molting.

Consider the recapture data for 1984 in Table 1. The relative abundance of animals with tag anchors loose in the body cavity and in the dorsal musculature, among animals which did not molt, is 14:29 or 0.48:1. Among animals which molted, the relative abundance is 1:16

Table 2

Incidence of necrosis around the tag anchor in male *Chionoecetes opilio* tagged in Conception Bay, Newfoundland, with t-bar tags.

	Tagging location			
	Dorsal muscle	Body cavity	Shell	Leg muscle
Number with necrosis	11	4	7	7
Number without necrosis	45	14	22	25
% necrotic	20	22	24	22

or 0.06:1. Hence animals with anchors loose in the body cavity appear to have become less abundant relative to those tagged in the dorsal musculature, and this suggests lower tag retention and/or lower survival for animals with anchors loose in the body cavity. In fact, the relative retention/survival rate can be estimated from the 1984 data as

$$\alpha = \text{relative retention/survival (loose:dorsal)} = \frac{\frac{1}{16}}{\frac{14}{29}} = \frac{1 \cdot 29}{16 \cdot 14} = 0.13.$$

The estimator α is the cross-product ratio frequently used in survival analysis (Fienberg 1980).

If all data were collected from animals tagged in the same year, then it would be a simple matter to use a χ^2 test to test the null hypothesis that the proportions in each location are the same for the two molt states (molted versus did not molt). However, animals were tagged in two separate years and there is at least a reasonably strong possibility that the tagging procedure varied between the years, e.g., due to developing tagging skill. This suggests that the interaction terms involving year may be significant. If interaction terms are ignored and the data from different years are pooled, then associations between variables (i.e., between molt status and tagging location) can be distorted and the apparent direction of the association can even reverse (see Fienberg 1980, chap. 3). An analysis which explicitly accounts for this possibility can be conducted using hierarchial loglinear models.

The 16 counts in Table 1 for individual years 1983 and 1984 can be envisioned as comprising a $2 \times 2 \times 4$ contingency table with main effects (categorizations) due to year of tagging (Yr), molt status (Molt), and location of tag within the body (Loc). There are nine loglinear models that can be fitted to these data (Table 3) ranging from the model of complete independence through seven models of partial dependence to the completely saturated model (see Fienberg 1980 for a discussion). The contingency table can be collapsed over the year variable if one (or both) of the two-factor interactions involving year is not significant. The hypothesis that tagging location has no influence on retention/survival through molt can be rejected if it is necessary to have an interaction between location and molt status (Loc * Molt) to have a good fit to the data.

Even the simplest model of main effects only (model 1) is not rejected by the likelihood ratio test ($P = 0.2067$, Table 3). It is still of interest to explore how strong the evidence may be that location of the tag affects survival/retention through the molt. We will therefore examine the following four models in more detail.

model 1:
  Count = [Molt] [Yr] [Loc]
model 3:
  Count = [Molt] [Yr] [Loc] [Yr] * [Loc]
model 4:
  Count = [Molt] [Yr] [Loc] [Molt] * [Loc]
model 5:
  Count = [Molt] [Yr] [Loc] [Molt] * [Loc] [Yr] * [Loc]

Table 3

Loglinear model analysis of tagging count data in Table 1. C is the predicted count, [Yr] represents year of tagging, [Molt] represents molt status, and [Loc] represents location of the tag anchor within the body. Asterisk (*) indicates an interaction between variables. To make the notation more compact, only the highest-order interactions are given for each variable. For example, the model C = [Loc] [Yr] * [Molt] represents main effects for location, year, and molt, plus the interaction between year and molt. The order of presentation of the variables has no significance in the model notation.

Model	Likelihood (χ^2)	df	P
1) C = [Yr] [Molt] [Loc]	13.31	10	0.2067
2) C = [Yr] * [Molt] [Loc]	13.30	9	0.1495
3) C = [Molt] [Yr] * [Loc]	7.03	7	0.4262
4) C = [Yr] [Molt] * [Loc]	8.11	7	0.3233
5) C = [Yr] * [Loc] [Molt] * [Loc]	1.82	4	0.7688
6) C = [Yr] * [Molt] [Loc] * [Molt]	9.09	6	0.2313
7) C = [Molt] * [Yr] [Loc] * [Yr]	7.01	6	0.3196
8) C = [Molt] * [Yr] [Loc] * [Yr] [Molt] * [Loc]	1.81	3	0.6120
9) C = [Yr] * [Molt] * [Loc]	0	0	1.0000

The above model descriptions are a common way of representing loglinear models. Model 1 indicates that the logarithm of the count in any cell can be predicted as the sum of the main effects for molt status, year of tagging, and location, i.e., these factors act independently. Model 3 is the same as model 1 except that an interaction term (or dependency) between year of tagging and location of anchor is also needed to predict the counts. Model 4 has a similar interpretation but the logarithm of the count depends on an interaction between anchor location and molt status. Model 5 includes the interaction between year and location and between molt status and location. Thus, models 1 and 3 imply no differential survival/tag retention among tagging locations, whereas models 4 and 5 imply that tagging location has an effect on the probability of surviving a molt with the tag still in place.

The difference between models 1 and 3 is that model 3 implies that the proportions of animals tagged in each location varied between the two years while model 1 implies the same proportions occurred in both years. If year has no effect on location (i.e., the interaction between year and location is unimportant), then a test of the effect of location on survival/retention through molt can be achieved by comparing models 1 and 4. But, if the proportions tagged in each location varied among the years, then the comparison that isolates the effect of tagging location on survival/retention through molt is the comparison of models 3 and 5.

The choice between two nested models can be made on the basis of a likelihood ratio test by subtracting the log-likelihoods and referring to a χ^2 table with degrees of freedom equal to the difference in degrees of freedom for the two models. The computed test statistic for comparing models 1 and 3 is

$$\chi^2_{comp} = 13.31 - 7.03 = 6.28, \quad df = 10 - 7 = 3$$

and the resulting P-value is 0.099. We fail to reject model 1 in favor of model 3 at the 5% level and conclude that the evidence is not strong enough to conclude that the proportions tagged in each body location varied by year. However, the test results could be considered marginally or nearly significant.

The hypothesis of interest is whether the tagging location affects the survival/retention through molt. This can be accomplished by comparing models 1 and 4,

$$\chi^2_{comp} = 13.31 - 8.11 = 5.20, \quad df = 10 - 7 = 3,$$

for which the P-value is 0.1577. Alternatively, we can compare models 3 and 5 and obtain virtually the same results. Thus, the statistical evidence is not strong enough to conclude that location affects survival/retention through molt at the customary 5% level. However, in light of the small sample sizes and possible low power of the test, the results provide some evidence, albeit weak, that location may be important.

Since at least one two-factor interaction involving year is not significant in each of the models we considered, one can validly collapse the three-dimensional table over year to obtain a 2×4 table. The estimated relative retention/survival rates, α, can be computed from the pooled data (Table 1). Relative to animals tagged in the dorsal musculature, the tag retention/survival of animals with tag anchors loose in the body cavity, embedded in shell, and in the dorsal leg musculature are estimated to be 0.23, 0.95, and 1.10, respectively.

Although 18% of the dissected animals had some blackening around the anchor of the tag, only 2 animals (1.5%) had extensive areas of necrosis. All animals had been at liberty for at least a year. The proportion of animals with necrotic tissue did not appear to vary much among the different tagging locations (Table 2).

Discussion

Although the laboratory study indicated that tagged animals die at the time of molting if the tag anchor lodges in the basal leg musculature, there was no evidence of this in the field data. We hypothesize that this is because the field-tagged animals were larger than the laboratory animals, and larger animals may tolerate a tag in the leg musculature better than smaller animals. If relative retention/survival due to anchor location depends on size of the animals, then size category should be considered as another variable in the analysis. However, in our field study only animals in a narrow range of sizes (82–120 mm CW at tagging) were examined so that there seems little point in dividing the limited number of recaptures into size classes.

Since the field data indicate that having the end of the tag loose in the body cavity reduces the chances of recovering the animal with tag intact (α 0.23), and the laboratory data indicate that tagging in the basal leg musculature reduces recoveries, it seems prudent to try to insert the tag anchor into the dorsal musculature. Our lack of statistically significant results does not imply that tagging location is not a significant biological factor in determining the success of a tagging program. Rather, it may simply indicate that our sample sizes were inadequate to obtain strong evidence of the importance of location. We recommend that, prior to initiating a field tagging program, a few trial animals be sacrificed to determine how consistently the tag anchor is being placed into the targeted dorsal musculature.

The loglinear model approach we used is quite general and allows any number of covariates (such as size at the time of tagging) to be properly accounted for. For those who prefer a regression approach to data analysis, the same analyses can be cast as logit models (see Fienberg 1980, chap. 6).

The laboratory study by Hurley et al. (1990) suggested that tag insertion frequently results in extensive necrosis of the tissue and carapace around the anchor. This was not seen in the field data. We speculate that the decreased levels of necrosis in the field-tagged animals may be due to the lower water temperatures in Conception Bay (-1.2 to -0.5°C in the Bay versus 4–6°C in the laboratory study).

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Seasonal and Annual Variability in the Diet of California Sea Lions *Zalophus californianus* at San Nicolas Island, California, 1981-86

Mark S. Lowry
Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA
P.O. Box 271, La Jolla, California 92038

Brent S. Stewart
Sea World Research Institute, Hubbs Marine Research Center
1700 South Shores Road, San Diego, California 92109

Carolyn B. Heath
Fullerton College, 321 E. Chapman Avenue, Fullerton, California 92634

Pamela K. Yochem
Sea World Research Institute, Hubbs Marine Research Center
1700 South Shores Road, San Diego, California 92109

John M. Francis
Smithsonian Institution, National Zoological Park, Washington, D.C. 20008

California sea lions haul out and breed on islands along the Pacific coasts of southern and Baja California and in the Gulf of California. About half of all births occur in southern California waters (Fig. 1), principally at San Miguel and San Nicolas Islands (Stewart et al. In press). Some studies have shown that diet varies geographically, perhaps influenced by seasonal variability of various prey (Fiscus and Baines 1966, Ainley et al. 1982, Everitt et al. 1981, Hawes 1983, Antonelis et al. 1984, Aurioles et al. 1984, Antonelis et al. 1990, Lowry et al. 1990). Here we describe seasonal and annual variability in the diet of California sea lions that hauled out at San Nicolas Island from 1981 through 1986.

Methods

We collected sea lion scats every one or two months at several rookeries and hauling grounds at San Nicolas Island (Fig. 1). Scats were washed through nested sieves (mesh sizes of 2.8 mm, 1.5 mm, and 0.71 mm) to recover hard parts such as fish otoliths, cephalopod beaks (i.e., mandibles), shark teeth, and invertebrate exoskeletal fragments. We identified prey species by comparing those remains with museum and personal voucher collections.

The frequency of occurrence (FO) of each prey taxon was calculated as the proportion of scats in each sample that contained at least one hard part from a prey taxon. We pooled monthly samples into four groups: winter (December–February), spring (March–May), summer (June–August), and autumn (September–November). We tested the null hypotheses that frequencies of occurrence of the most common prey (those that occurred in 5% or more of all scats) did not differ among seasons nor among years using a two-way analysis of variance (Program 7D of BMDP-87; Dixon 1987); we excluded data for 1981 from this analysis because we lacked data for some seasons. We tested the null hypothesis that dietary diversity did not differ among seasons or among years using multiway contingency table analysis (Program 4F of BMDP-88; Dixon 1988).

Results

We examined 1232 scats from summer 1981 through autumn 1986; 1085 of those contained identifiable prey hard parts (Table 1). We identified 32 prey taxa to species and 6 to genus, but only two genera of cephalopods and five of fish occurred in 5% or more of the scats. Therefore, we confined our analyses of seasonal and annual variability in diet to the latter 7 taxa. Northern anchovy *Engraulis mordax* was the most common prey, occurring in about half (50.6%) of all scats; Pacific whiting *Merluccius productus*, jack mackerel *Trachurus symmetricus*, rockfish *Sebastes* spp., and market squid *Loligo opalescens* each occurred in about 22–30% of scats (Table 2).

We are limited in our generalizations about seasonal trends in the frequencies of occurrence of prey species because of strong seasonal-annual interactions (ANOVA, $P < 0.05$). There are, however, some differences apparent among some seasons and years (Fig. 2). Northern anchovy was eaten more often in winter than in other seasons in 1982, 1983, and 1984, but not in 1985 or 1986; anchovy was present in more than 60% of scats each season in 1986. Furthermore, anchovy occurred in scats more often from 1984 through 1986 than in earlier years. Pacific whiting was eaten frequently from summer 1981 through spring 1982, and in spring

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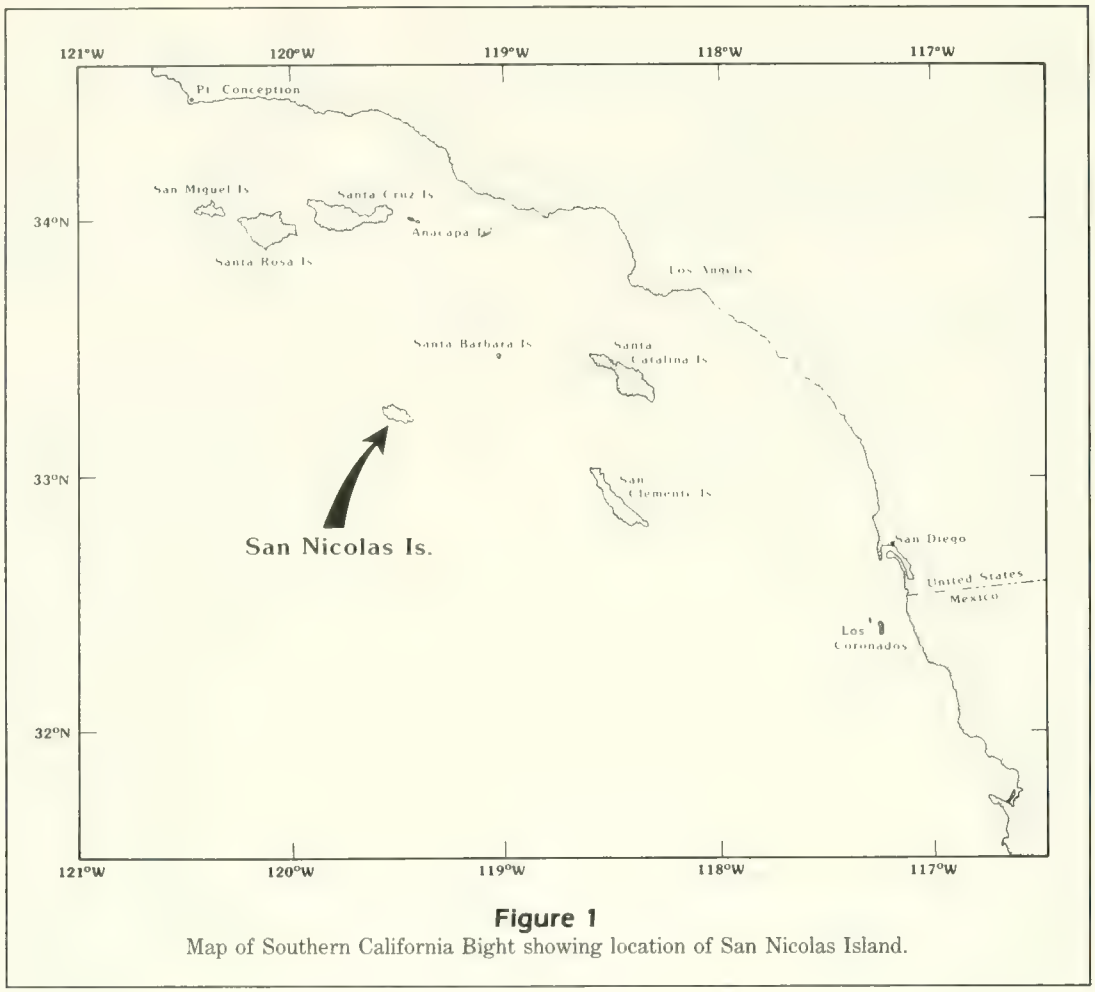

Figure 1
Map of Southern California Bight showing location of San Nicolas Island.

Table 1
Scat samples of *Zalophus californianus* collected at San Nicolas Island, California.

Year	Winter	Spring	Summer	Autumn	Total
1981	0	0	24	18	42
1982	12	15	68	13	108
1983	4	42	150	55	251
1984	75	35	107	93	310
1985	62	77	64	63	266
1986	35	24	80	116	255
Total	188	193	493	358	1232

1984 through spring 1985. Jack mackerel was found in scats more often in summer 1981 through autumn 1983 than after that period. Rockfish were commonly found in winter 1982, and spring 1984 through spring 1985. Market squid was more common in the diet prior to 1983 and its frequency of occurrence was higher in either autumn or winter, or both, each year except in 1984. Pelagic red crabs *Pleuroncodes planipes* appeared in scats in 1983, were frequently eaten through 1985, and then disappeared from the sea lions' diet. Pacific mackerel occurred frequently in summer and autumn 1982. *Octopus* spp. were eaten more often in spring 1984 than at any other time and appeared in the diet mostly in spring and summer of all years.

About 69% of all scats contained one or two prey taxa (Fig. 3). There were significant season-year interactions ($P<0.05$) for all years and seasons, but the number of prey taxa occurring in each scat was greatest from 1981 through 1984 and least in 1985 and 1986 (Fig. 3).

Discussion

California sea lions forage in a number of different habitats and depth strata in the Gulf of California and along the North American Pacific coast from Baja California to British Columbia. The composition of the sea lions' diet varies geographically (Jameson and

Table 2

Prey found in scat samples (n) and frequency of occurrence (expressed in %) for prey found in 1085 California sea lion scats collected at San Nicolas Island, California, 1981–86.

Prey			
Scientific name	Common name	n	%
Teleosts			
Engraulis mordax	northern anchovy	550	50.6
Merluccius productus	Pacific whiting	318	29.3
Trachurus symmetricus	jack mackerel	303	27.9
Sebastes spp.	rockfish	282	25.9
Scomber japonicus	Pacific (chub) mackerel	123	11.3
Chromis punctipinnis	blacksmith	22	1.9
Oxyjulis californica	señorita	15	1.3
Porichthys notatus	plainfin midshipman	5	0.4
Cololabis saira	Pacific saury	5	0.4
Icichthys lockingtoni	medusafish	5	0.4
Lycodes cortezianus	bigfin eelpout	4	0.3
Chilara taylori	spotted cusk-eel	3	0.2
Microstomus pacificus	dover sole	3	0.2
Citharichthys spp.	sanddab	3	0.2
Cymatogaster aggregata	shiner surfperch	3	0.2
Zalembius rosaceus	pink seaperch	3	0.2
Lyopsetta exilis	slender sole	2	0.2
Leuroglossus stilbius	California smoothtongue	2	0.1
Symbolophorus californiensis	California lanternfish	2	0.1
Sardinops sagax	Pacific sardine	2	0.1
Phanerodon furcatus	white seaperch	2	0.1
Zaniolepis spp.	combfish	2	0.1
Citharichthys sordidus	Pacific sanddab	2	0.1
Girella nigricans	opaleye	1	0.1
Medialuna californiensis	halfmoon	1	0.1
Argentina sialis	Pacific argentine	1	0.1
Stenobrachius leucopsarus	northern lampfish	1	0.1
Anoplopoma fimbria	sablefish	1	0.1
Icelinus tenuis	spotfin sculpin	1	0.1
Unid. Myctophidae	lanternfish	10	0.9
Unid. Embiotocidae	surfperch	3	0.2
	unid. fishes	72	6.6
	unid. flatfish	3	0.2
Elasmobranchs			
Prionace glauca	blue shark	1	0.1
Cephalopods			
Loligo opalescens	market squid	238	21.9
Octopus spp.	octopus	70	6.4
Onychoteuthis borealijaponicus	squid	52	4.7
Abraliopsis spp.	squid	24	2.2
Gonatus spp.	squid	18	1.6
Gonatopsis borealis	squid	13	1.1
Chiroteuthis calyx	squid	1	0.1
Unid. Gonatidae	squid	4	0.3
	unid. cephalopod	20	1.8
Crustaceans			
Pleuroncodes planipes	pelagic red crab	118	10.8
	unid. crustacean fragments	5	0.4
Algas			
Unid. Algae	algae	6	0.5

Kenyon 1977, Bowlby 1981, Everitt et al. 1981, Jones 1981, Bailey and Ainley 1982, Antonelis et al. 1984, Aurioles et al. 1984, Roffe and Mate 1984), but dietary diversity appears to be rather low in each location relative to the number of prey taxa consumed rangewide. Our studies of seasonal and annual variability in diet of sea lions at San Nicolas Island further support the classification of California sea lions as plastic specialists (Morse 1980). California sea lions exploit a few resources at a time, but prey composition of the diet is temporally dynamic; they capitalize on the more seasonally abundant and accessible schooling or aggregating prey.

The dietary occurrence of the sea lions' primary prey (northern anchovy, Pacific whiting, rockfish, jack mackerel, and market squid) appears to be related to the seasonal and annual occurrence of those prey species near San Nicolas Island. Market squid were eaten most often in autumn and winter in most years corresponding with the seasonal nearshore movements of spawning squid in this area (Bedford et al. 1983, Klingbeil 1986). Market squid were not commonly eaten by sea lions in 1983 and 1984, a time when squid were uncommon in the Southern California Bight (cf. Bedford et al. 1983; Klingbeil 1984, 1985, 1986; Grant 1987).

The presence of northern anchovy in the diet of sea lions seems to be related to the availability of anchovy near San Nicolas Island. Northern anchovy were uncommon near San Nicolas Island from 1982 through 1984, but were quite abundant in that area in 1985 and 1986 (Bindman 1986, Methot and Lo 1987). Sea lions consumed northern anchovy frequently in all seasons in 1985 and 1986, but substantially lower from 1981 through 1984, except during winter when anchovy were spawning and evidently nearer to San Nicolas Island than in other seasons.

The number of prey taxa eaten appears to be closely linked to the abundance and availability of northern anchovy. When anchovy were abundant near San Nicolas Island, sea lions evidently ate them in preference to other species. Both seasonal and annual patterns indicate that when the frequency of occurrence of anchovy in the diet is high, the number of prey species consumed is low. When northern anchovy are not available the breadth of the diet increased, with 3 to 4 other species being eaten.

Jack mackerel were displaced northward out of the Southern California Bight in 1984 when ocean surface currents changed and warm water associated with the 1982/83 El Niño-Southern Oscillation intruded into that area from Baja California (Mason 1989); the presence of jack mackerel in sea lion scats declined substantially then. Pelagic red crabs were transported into the Southern California Bight during this warm-water intrusion and they were frequently eaten by sea lions in 1983 and, to a lesser extent, through 1985 when they disappeared from their diet.

The dietary and behavioral flexibility of California sea lions in response to movements and availability of prey and to environmental perturbations (e.g., El Niño Southern Oscillation) may be one of the most important factors contributing to the consistent increase in their abundance during the past several decades. Relative to other locations, it appears that northern anchovy may be one of the most important prey of California sea lions near San Nicolas Island. This regional phenomenon is due to the proximity of San Nicolas Island to large spawning aggregations of northern anchovy compared with other locations where dietary studies of California sea lion have been made.

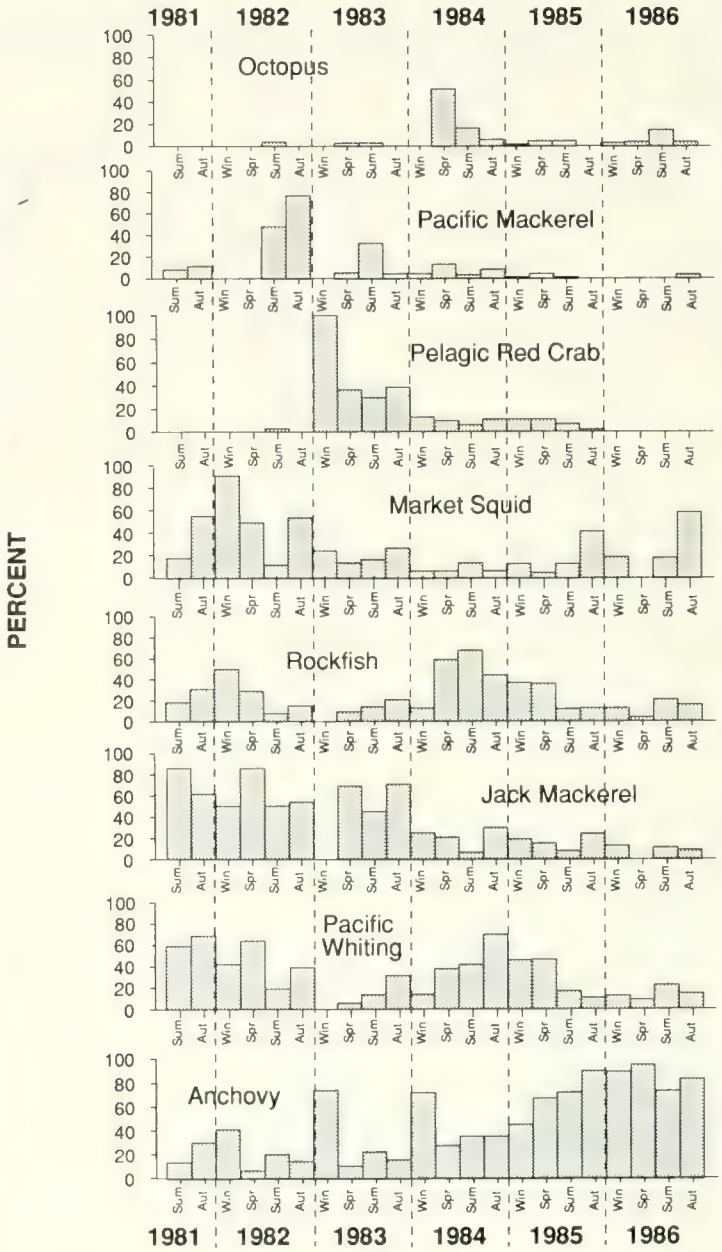

Figure 2

Seasonal frequency of occurrence (%) for eight prey taxa found in California sea lion scats collected at San Nicolas Island, California.

Acknowledgments

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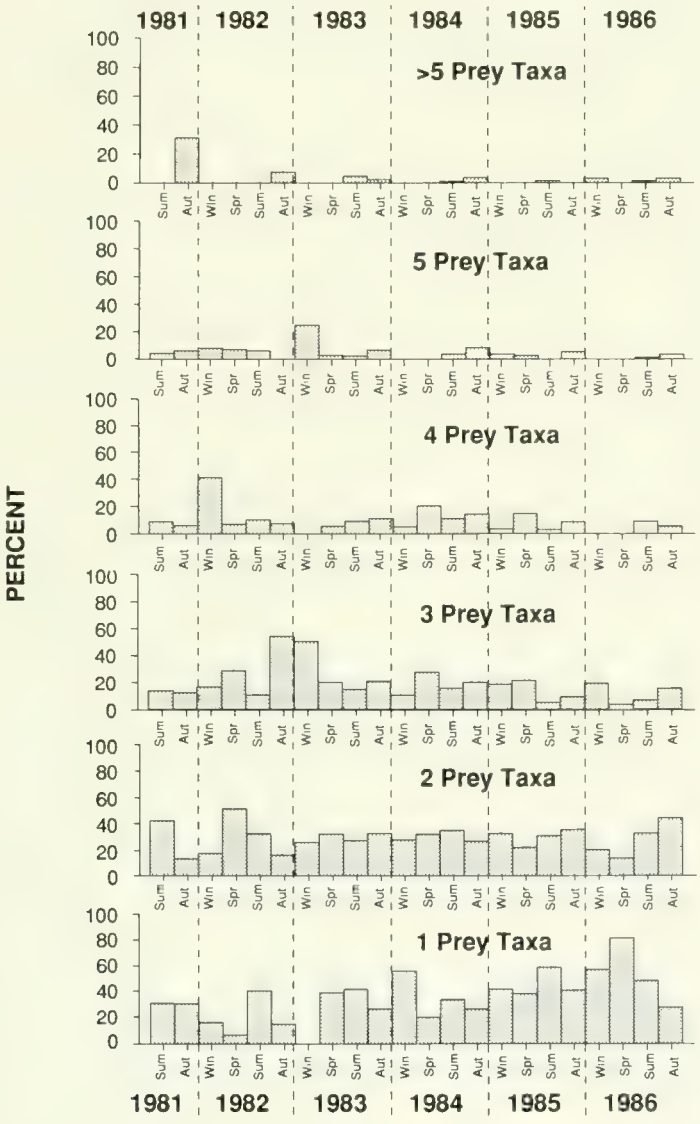

Figure 3

Frequency distributions of the numbers of prey taxa found in California sea lion scats collected at San Nicolas Island, California, summer 1981–autumn 1986.

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Automated Enumeration by Computer Digitization of Age-0 Weakfish *Cynoscion regalis* Scale Circuli*

Stephen T. Szedlmayer
Margaret M. Szedlmayer
Auburn University, Marine Extension and Research Center
4170 Commanders Drive, Mobile, Alabama 36615

Michael E. Sieracki
Virginia Institute of Marine Science,
College of William and Mary, Gloucester Point, Virginia 23062

There has been extensive use of daily otolith growth increments in age and growth studies of age-0 fishes (Campana and Neilson 1985). Recently, the daily ageing method has been extended to scales (Szedlmayer et al. In press). However, visually counting increments is tedious, time consuming, and subject to human error (Rice 1987). In an effort to automate the counting of increments or daily circuli in scales of age-0 juvenile weakfish *Cynoscion regalis*, a microcomputer-based system was used to digitize the video image of a scale, store the light intensities from a radial transect, and count circuli. Circuli were also counted visually to verify the accuracy of the software. Others have used microcomputer-based systems to aid in increment counting (Tzeng and Yu 1988, Thorrold and Williams 1989, Karakiri et al. 1989), but to our knowledge the present algorithm is the first method that completely automates increment counting with a high degree of accuracy.

Materials and methods

Age-0 juvenile weakfish were collected from the York River, Virginia (for further collection methods, see Szedlmayer et al. 1990). Fish, 50–140 mm standard length (n = 45), were anesthetized with tricane methanol sulfate (50 mg MS-222/L seawater), and scales removed from just below the midbody lateral line curve. The scales were placed on a glass slide in water and cleaned with a paint brush, then permanently mounted with a methacrylate copolymer, and covered with a glass cover slip (Flo-Texx liquid cover slip, Lerner Lab.).

For the visual method, scale circuli were counted twice by the same reader, along a central radius from the focus to the edge, on the anterior side, at 125× magnification on an Olympus BH-2 microscope. If counts were not the same, they were counted a third time. Only 1 out of 45 required a third count, and for that scale the counts that were the same were used for comparison with automated computer counts.

For automated counting, scales were digitized using the same magnification and radius as visual counts. Scale images were detected by a Ikigami ITC-510 video camera (625-line resolution) mounted on the microscope, digitized by a Matrox PIP-512B image analyzer, and stored in computer memory in a matrix of 512 × 512 picture elements (pixels) with 256 gray levels for each pixel. A PC-AT 286 computer with a 10-meg Hz processor, 1-meg RAM, and math coprocessor controlled the image analyzer. A 40-megabyte hard disk and a floppy disk drive were used for image and data storage.

Once the image was digitized, it was displayed on a Panasonic PM 205A video monitor (1000-line resolution) and a mouse was used to control the movement of a cursor mark projected on the image. The cursor was then positioned to select two points defining a transect from the focus to the edge of the scale perpendicular to the circuli (Fig. 1). Light intensities (gray levels) of three transects, each one pixel apart and one pixel wide, were simultaneously stored to the hard disk. Each transect was then analyzed using a Fortran program to identify and count scale circuli. The algorithm applied a moving average (7, 8, 9, and 10 pixel averages were tried) to smooth each transect and then searched for local minima (e.g., 10 pixels on either side of the inflection point corresponds to a local minimum within a search width of 20 pixels; search widths of 18, 20, 22, and 24 pixels were tried). The Fortran counting algorithm compared adjacent pixels and determined if light intensity increased or decreased. Subsequently, an increment was counted only after the following two criteria were satisfied: (1) an inflection point was detected, i.e., a change in light intensity from decreasing to increasing, and (2) the inflection point was the minimum light intensity within the specified search width. Depending on the scale size, one to five images were needed to complete a scale count (i.e., with smaller scales the complete scale was included in the digitized image, but with larger scales several images were needed at the same magnification to include all circuli from the focus to the edge). The computer counts (aver-

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Figure 1
Photograph of a weakfish scale with 29 circuli (29 circuli + edge = count of 30). Arrow depicts counting transect from focus to perimeter along the anterior growing side (transect line = 0.5 mm).

ages of the three counts from individual scales) were then regressed against the visual counts.

Results and discussion

Application of a nine-pixel smoothing interval on the transect data combined with a 20-pixel local-minima search width, produced the highest coefficient of determination (r^2 0.99) between the automated and visual counts (Fig. 2). Other combinations of smoothing interval and search width resulted in lower coefficients. The present program allows adjustment of smoothing interval and search width to optimize its use with other fish species. Computer counting was approximately 3.3 times faster than visual counting. The visual method showed a slightly higher precision compared with computer counting, but savings in time more than compensates for this small increase in error (Table 1). In addition, the concentration needed and subsequent fatigue in visual counting compared with computer counting are difficult to measure, yet computer counting was considered much easier by all scale readers.

Microcomputer systems that can digitize increments from scales, otoliths, and other bony structures have been previously reported and demonstrated potential for automated counting (McGowan et al. 1987). The present system makes an advance over other systems by using the local-minimum method of increment identification. Previous methods usually use threshold-light intensity levels to identify increments that may produce discrepancies between computer

Table 1
Comparison of counts and counting times of scale circuli from weakfish *Cynoscion regalis* between computer and visual methods from a random subsample of those counted. Each scale was from a different fish.

	Visual counts				Computer counts				
Scale	1st	2d	3d	Time (s)	1st	2d	3d	$\bar{x}$	Time (s)
1	36	36		46	38	38	38	38.0	13
2	32	32		42	31	31	32	31.3	16
3	32	32		41	31	32	33	32.0	13
4	37	37		46	39	38	38	38.3	12
5	32	32		42	31	31	32	31.3	16
6	30	30		39	30	30	30	30.0	12
7	50	51	50	106	51	52	50	51.0	13
8	60	60		82	64	62	61	62.3	35
9	46	46		51	48	47	49	48.0	19
10	43	43		45	44	44	44	44.0	15
11	58	58		94	60	60	60	60.0	26
12	64	64		74	66	67	65	66.0	25
13	60	60		80	61	58	61	60.0	31
14	49	49		56	50	50	50	50.0	15
15	58	58		69	60	58	58	58.7	14
				$\bar{x}$ 60.9					$\bar{x}$ 18.3
				SD 21.7					SD 7.4

Paired t-statistic = 8.85, t critical value (level = 0.05) = 2.145, therefore there is a significant difference between counting time.

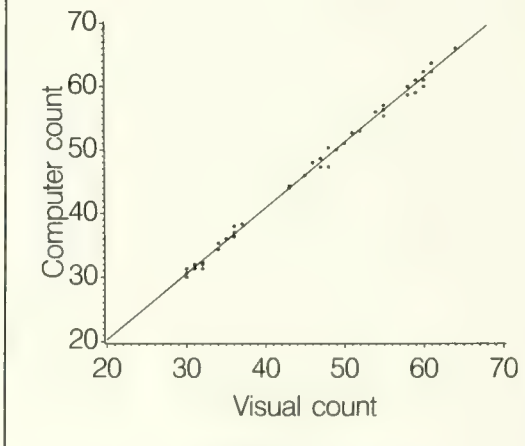

Figure 2
Linear regression of computer automated count on visual count of scale circuli from weakfish, *Cynoscion regalis* (N 45 fish, r^2 0.99, $y = 1.03x - 0.3$).

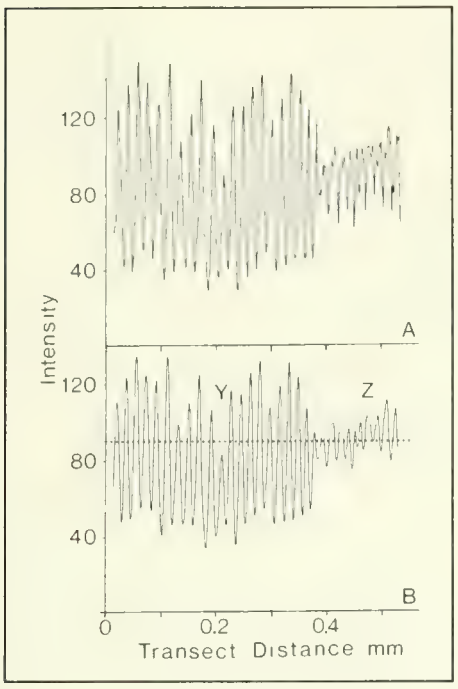

Figure 3

Light intensities along a transect taken from a single scale by distance in mm. (A) Light intensities of a single transect. (B) Smoothed data using a nine-point moving average. Dashed line represents a threshold light intensity of 90. Lowering the threshold to include peak Y would eliminate peaks under Z.

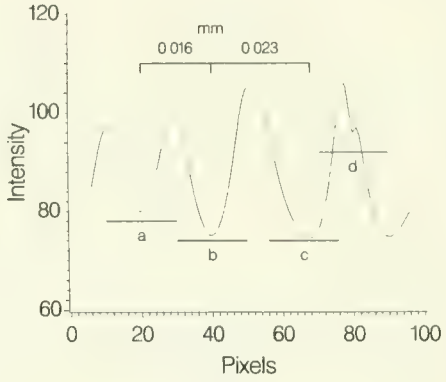

Figure 4

Light intensities from a section of a scale transect enlarged to illustrate pixel spacing. Circuli spacing changed, but each minima (a, b, and c) were only counted once. Inflection point (d) was detected but not counted as a circulus, because it was not a local minimum in a 20-pixel search width. Horizontal lines above letters represent search width size = 20 pixels.

and visual counts, because background intensity levels change as the transect moves across the otolith or scale. Thus, some areas may be counted incorrectly when they fall below the selected threshold level as shown for a transect across a weakfish scale (Fig. 3). The local-minimum method solves this problem, since identification of increments is only dependent on adjacent pixel-light intensity levels. The local-minimum method also responds to changes in increment spacing: as increment spacing increases (measurements from one typical scale ranged from 10.3 to 22.9 m^{-6}) the algorithm moves greater distances (more pixels) along the transect, but does not count more increments until another minimum is detected. For example, in Figure 4, increments a, b, and c were each counted as one circulus despite changes in circuli spacing, but inflection point d was not counted because it was not a local minimum within a 20-pixel search width.

Increments narrower than the selected search width would cause errors (e.g., microincrement spacing width = 10 pixels, but search width = 20 pixels). However, this problem can be corrected in three ways: (1) reduce the search width; (2) increase the magnification of the scale or otolith, e.g., from 125 to 400; or (3) increase the number of pixels between increments, i.e., increase the resolution of your system as discussed below. In addition, the true limit of counting narrow increments is not the algorithm, but the resolution limit of the light microscope. After projection of the image onto the video monitor, one pixel corresponds to an actual distance of about 0.2 m^{-6} (with the light microscope at 1000×). This 0.2 m^{-6} size is the maximum theoretical resolution of any light microscope (Eastman Kodak Co. 1980). In addition, "...the functional limits are invariably higher than those derived theoretically" (Campana et al. 1987), therefore several pixels may be present even between the smallest detectable increments. Other advantages of the present system, as well as other systems, include elimination of data entry and associated transcriptional errors, and establishment of repeatable criteria for ageing of fishes.

A disadvantage of the present system and other similar systems is that clearly defined increments are needed. This was not a problem with weakfish scales because circuli are distinct (Fig. 1), but application to otolith increments may need further refinement. Another disadvantage is that most systems need multiple images to complete a transect reading of a single scale or otolith, which may increase processing time and errors. The multiple-image-per-transect problem results from a limiting number of pixels (512 × 512 pixels) in our digitizer, such that lower magnifications (25 or 40) that would encompass the entire transect do not contain enough pixels for accurate identification of increments. Systems with greater pixel resolution (e.g., 1024 × 1024) would alleviate this problem, and are now commercially available.

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Abstract.– Yellowfin tuna *Thunnus albacares* are commonly found associated with other species, especially sharks, birds, and dolphins, in the eastern tropical Pacific. Data from the purse seine fishery there, collected during 1974 and 1975, indicate that sharks occurred with tuna in 40% or more of the purse seine sets made around floating logs. Most other species, including rays, billfish, and small tunas, usually occurred in less than 10% of the sets. The association rate of these bycatch species declined progressively from log- to school- to porpoise-associated sets. This, together with their behavior as understood, suggests that at least some of these species stay with the tuna as much as they can. Such behavior would be like that of polyspecific associations in which two or more species travel together for foraging and protective advantages.

Polyspecific Nature of Tuna Schools: Shark, Dolphin, and Seabird Associates

David W. Au

La Jolla Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271, La Jolla, California 92038

Tuna are often found associated with other species, a behavior that is also seen among other schooling, herding, or flocking animals. While it is often convenient to think of any of these species as being effectively monospecific (single species) in behavior, there is growing awareness that polyspecific, enduring assemblages are common among higher animals. Such associations, comprised of several species that feed, interact, and travel together for periods of time, are not merely aggregations of animals along routes or points of common attraction. The specific interactions involved are not well understood, even though field observations have been intensive in some cases.

Mixed-species schools of fishes are frequently observed and caught. While usually seen as chance associations (e.g., Itzkowitz 1977), some species in these schools may obtain enhanced protective and foraging benefits (Ehrlich and Ehrlich 1972, Barlow 1974, Wolf 1987). Many such schools may therefore be polyspecific, and represent purposeful interactions.

Polyspecific bird flocks are common (Moynihan 1962; Morse 1970, 1977; Munn and Terborgh 1979). In some cases, over a dozen species move together through different environments with the composition of individuals and species apparently changing little (Hutto 1987). Diamond (1981) pointed out that polyspecific flocks often consist of similar core species that stay together, perhaps for years, maintaining flock characteristics and holding group territories. There are leader species, which are usually conspicuous, and follower species (Caldwell 1981, Greig-Smith 1978).

Mammals, with even more complex behaviors, abound with examples of polyspecific associations. Such associations have been noted in bats, cetaceans, often in ungulates, and particularly in the behaviorally versatile primates. Among the latter, species pairs of certain cercopithecid monkeys may be together 50% of the time, and it often appears that one species initiates and terminates the association, and uses the other to better discover food and detect danger (Struhsaker 1981, Cords 1987). Locally, these polyspecific associations are species-specific; other sympatric monkeys are apparently ignored and always by themselves (Gautier-Hion et al. 1983). This suggests that benefactor species are actively searched for by follower species. These associations, which vary in species composition by area, may last for days or months. Group territories may be defended. Similar behaviors have been observed in cebid monkeys, some of whose polyspecific associations appear to be permanent (Terborgh 1983). Interestingly, monkey species that appear to initiate and benefit from the polyspecific associations can be observed sometimes in front, sometimes at the rear, of traveling groups.

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In general, polyspecific associations seem to form when social species of similar foraging ecology join to form larger groups to increase feeding success and to better avoid predators. The former may be ascribed to facilitation of feeding or to greater access to resource information (Clark and Mangel 1984). An additional benefit might be a lessening of intragroup competition (relative to monospecific groups of the same size). The enhanced safety could result from more effective vigilance (Pulliam 1973) or to the "convoy" effect (Olson 1964). It seems that the behaviorally more versatile species often exploit other species' behaviors, although there appear to be mutual benefits as well. For the most part, these polyspecific associations seem loosely coupled; the overt interspecies behaviors are circumstantial rather than obligatory, and generally agonistic. Species appear to join and leave the groups mainly in response to foraging situations; accordingly, they may be together for hours or days, sometimes months or even years.

In this paper I describe species found with tuna in the eastern tropical Pacific (ETP) and propose that tuna schools have a polyspecific nature. What this implies about tuna biology, especially that of the yellowfin *Thunnus albacares*, is discussed.

Data and methods

I used data collected by Southwest Fisheries Science Center (SWFSC) observers placed aboard U.S. tuna purse seiners. Such data have been available since 1966, but the records have not always been consistent or extensive with respect to other species caught with tuna (except for dolphins). The reasons include the pressure of observers' duties and the proprietary nature of fishing operations. After 1975, some kinds of bycatch information were no longer collected at all, and only abbreviated codes for certain other associated species were recorded.

The earlier, pre-1976 observer records, however, contain many candid notes on bycatches and other tuna associates, although even then the logs required only generic, not comprehensive, descriptions. Fortunately, some observers clearly were interested in tuna-associated fauna, and they frequently recorded detailed descriptions of what they saw.

I therefore selected records from the more information-rich 1974–75 database on purse seine sets (a "set" is a launch and retrieval of a purse seine net) for information on species that occur with tuna. I compiled a list of 22 observers personally known by myself or other SWFSC workers to have been reliable or to have had keen interest in pelagic fauna, and obtained pertinent information from their original logsheets. These logsheets constituted the set records of each of their 33 fishing trips. The trips occurred during all months except December, with 90% of the data collected between January and mid-June.

I examined the data pooled over all fishing trips and also by individual trip, since the quality of the records varied among observers. The data from one T.M. Duffy (TMD) is presented separately in the analysis below (TMD sets cf. the regular fleet sets) to illustrate how the actual observations of a particular observer could differ from the overall, pooled results. Duffy recorded information copiously and was an experienced and interested observer.

The data were divided into two areas and according to how the tuna were caught. The areas, delimited by latitudes 15°S and 25°N, were from the Central American coasts westward to 100°W ("off Central America") and from 100°W out to 135°W ("off Mexico") (see Figure 1). The first area contained sets mainly off the Central American coasts and southwestward to the Galapagos Islands; this is an important area for fishing both free-swimming and log-associated tuna, and also dolphin-associated tuna (explained below). The second area had sets mainly between southern Mexico and Clipperton Island, where much dolphin-associated tuna is taken. The tuna sets were further partitioned according to whether they were made around floating logs ("log–fish" sets), on free-swimming tuna ("school–fish" sets), or on dolphin-associated tuna ("porpoise–fish" sets). These are the terms used by the fishermen for the variously caught tuna, i.e., for different set types. The porpoise–fish sets refer to tuna caught usually with spotted and spinner dolphins, *Stenella attenuata* and *S. longirostris* (called "porpoise"). Table 1 gives the numerical breakdown of the 1762 purse seine sets I examined according to the above categories.

The purse seine sets in each area and set-type category were examined for frequency of different associated species to obtain a profile of the multispecies composition of the tuna schools. For each of certain species—actually grouped species because identifications were inexact—this frequency was expressed as the fraction (p) of the pertinent sets in which the species was caught. For comparison, I calculated both overall fractions considering all sets from all trips and arithmetic means of the fractions for individual trips. The latter fractions were computed only where fishing trips had more than ten sets in the category of interest. Binomial 95% confidence limits of the overall fractions were determined in accordance with the number of sets involved (n). Ranges were determined for the trip fractions. These latter fractions were statistically heterogeneous among trips, at least for log–fish and porpoise–fish sets. Thus the overall fractions probably best reflect the polyspecific composition of schools.

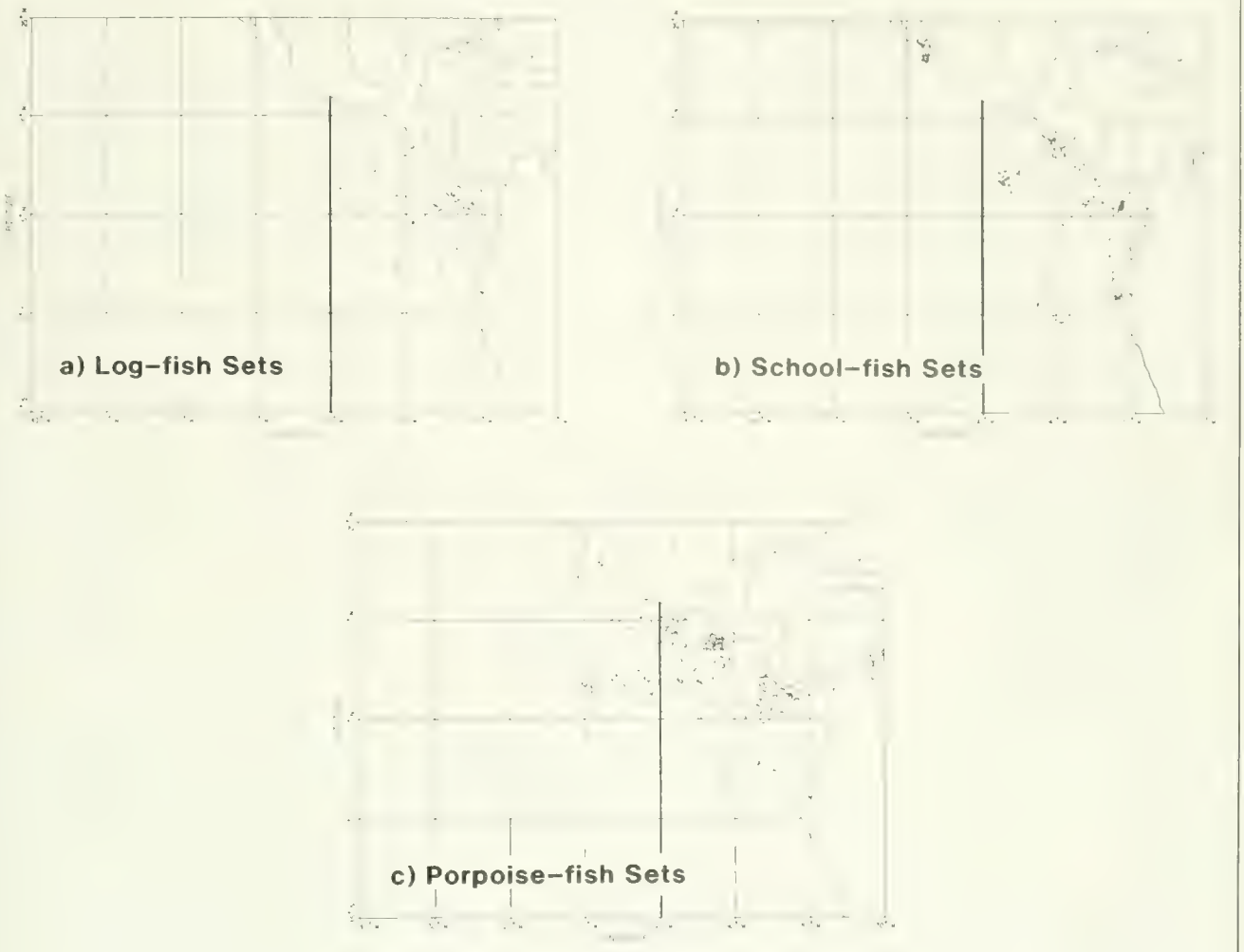

Figure 1

Locations of (a) log–fish sets, (b) school–fish sets, and (c) porpoise–fish sets inspected. Data were examined separately to the east ("off Central America") and west ("off Mexico") of longitude 100°W.

Related data gleaned from the records were summarized. These included information on size, abundance, and actual species composition within the species groups.

The species composition of bird flocks occurring with the tuna was described after ordering the (n) reported species in each flock according to (1 to n) decreasing ranks of abundance (again, the species were actually grouped species). This was done to circumvent differences in the accuracy with which different observers estimated species' flock sizes. The fraction of total flocks in which a bird species ranked at least 2 (i.e., was at least second most-abundant) was regarded as that species' importance value. When that value was 50% or more of the flocks in a category, that species was considered dominant for that set-type category. Several species could be "dominant" according to this criterion.

Both yellowfin, and skipjack *Katsuwonus pelamis*, tuna are sought by purse seiners, although yellowfin is usually preferred. Overall, yellowfin was captured in 78% of the log–fish sets, 57% of school–fish sets, and 99% of porpoise–fish sets examined (including sets capturing both tunas). The mean tonnages of yellowfin caught per set, based on "successful sets," are given in Table 1. Successful sets are those catching more than 1 ton of yellowfin and/or skipjack tuna.

Tunas from the different set types are likely to behave differently, since younger yellowfin tend to associate with floating logs in nearshore waters while older, larger fish tend to be with dolphins farther offshore (Greenblatt 1979). Therefore, the species associations

Table 1

Characteristics of yellowfin tuna sets examined for other-species associations according to log-fish, school-fish, and porpoise-fish set types.

		Off Central America			Off Mexico		
		Log	School	Porpoise	Log	School	Porpoise
Fleet data	Total sets	185	438	540	2	104	220
	SS Ratio[1]	0.69	0.61	0.80	—	0.54	0.92
	YF tons[2]	6.5	6.8	8.9	—	5.7	8.2
	(n)	102	145	379	—	51	192
	2 SE[3]	1.3	1.2	1.1	—	1.5	1.2
TMD[4] data	Total sets	58	65	78	1	1	70
	SS Ratio	0.74	0.57	0.85	—	—	0.83
	YF tons	6.0	7.5	11.8	—	—	7.4
	(n)	34	22	49	—	—	60
	2 SE	1.4	1.7	1.3	—	—	1.3

[1]The Successful Set (SS) Ratio = fraction of total sets catching more than 1 ton of yellowfin and/or skipjack tuna. On porpoise-fish sets, the SS Ratio pertains to sets on *Stenella* dolphins only.
[2]Geometric mean short tons of yellowfin tuna (YF) per set, based on successful sets only; n is the size of the sample. Not all successful sets caught yellowfin.
[3]The multiplication-division factor for mean YF tons/set giving its 95% confidence interval.
[4]Observer T.M. Duffy (fleet data exclude these data).

with tuna, as seen in this study, will be discussed in terms of the ontogeny of yellowfin behavior.

Results

The fractions (p) of purse seine sets measuring the association rates of different (grouped) species are given in Table 2 (off Central America) and Table 3 (off Mexico). These fractions (expressed as percentages) are for the fleet sets, and they are summarized graphically in Figure 2. Figure 3 shows the association fractions for the T.M. Duffy (TMD) sets. In the tables, those species whose association rates differed significantly (χ^2, $P<0.05$) among set types are indicated by asterisks. For these, one can determine which of the set types was actually different by noting which of the mean rates occurred outside the 95% confidence intervals for the other set types.

Sharks clearly stood out among the fishes found associated with tuna. Overall, 40% of log-fish tuna sets took sharks. There was a progressive decline in this percentage to 10%, from log- to school- to porpoise-fish sets. Off Mexico, however, porpoise-fish sets may have been more likely to catch sharks (lower graphs in Figures 2 and 3). How commonly sharks may associate with tuna is emphasized by the TMD data (Fig. 3); individual fishing trips, of which this data from a single observer are an example, can experience shark occurrence rates of up to 90% on log-fish sets. The silky shark *Carcharhinus falciformis* was the most commonly reported species (25.2%) (Table 4). These sharks averaged 29.2 individuals in sets that caught them. However the range was large, from 1 to 500 per set. Other carcharhinids recorded were each under 10% of the identified sharks. Of these, the whitetip shark, frequently recorded with porpoise-fish sets (especially off Mexico), was most likely the oceanic whitetip *C. longimanus*, (R. Rasmussen, SWFSC, pers. commun.). Other less-common sharks included the whale shark *Rhincodon typus*. This species can be locally common off Baja California, where it is often associated with skipjack tuna. Sizes of the sharks caught with yellowfin were seldom recorded; however, it is known that medium- to large-sized specimens that are considered dangerous are often caught. The few sizes recorded ranged from 1.7 to 2.1 m. Many were simply described as "large." Others, described as "small" or comprising "25 tons" of catch, were probably all small-sized.

Rays occurred mainly in school-fish and porpoise-fish sets, the former more often. The records indicate that most were medium- to large-sized manta rays (Mobulidae). They occurred in groups of 1 to 2 on average, though up to 12 were recorded in some sets (Table 4).

Billfish (Istiophoridae) co-occurred with tuna in about 9% of the sets overall and more often off Central America than off Mexico. The association rates were similar among all set types, except for the TMD data

Table 2

Fraction (p) of purse seine sets (n) having various associated "species," off Central America (coast to 100°W).

		Fleet sets[1]						
		Overall fraction			Mean of trip fractions			
Associated spp.	Set type[2]	p (%)	n	95% CI[3]	p (%)	n/T	Range (%)[3]	Comments
Birds	L	83*	185	76–89	79	144/8	36–100	Birds very common with schools. Virtually all porpoise–fish sets are with birds.
	S	80	438	75–84	82	404/13	43–100	
	P	98	540	96–99	98	497/17	89–100	
Sharks	L	40*		32–48	37		21–77	Sharks common to very common with log–fish sets, but decreasingly so from log– to school– to porpoise–fish sets.
	S	21	"	17–26	20	"	0–61	
	P	13		10–17	13		0–36	
Rays	L	1*		0–3	1		0–7	Rays more often with school–fish sets than with porpoise–fish; rather seldom with log–fish.
	S	10	"	7–13	10	"	2–18	
	P	5		3–8	4		0–18	
Billfish	L	8		5–13	7		0–25	Billfish sometimes more frequent with log–fish sets, otherwise, similarly frequent among all school types.
	S	9	"	6–12	11	"	3–35	
	P	9		6–12	7		0–23	
Bullet tuna	L	10*		6–16	8		0–23	Bullet tuna often with logs; decreasingly so with school– and porpoise–fish sets.
	S	4	"	2–6	4	"	0–17	
	P	1		0–3	<0.5		0–5	
Black skipjack	L	12*		7–18	15		0–40	Black skipjack more often with log–fish sets; not with porpoise–fish.
	S	5	"	3–8	5	"	0–19	
	P	0		0–1	<0.5		0–2	
Turtle	L	3*		1–7	4		0–9	Turtles infrequent and without trend among the different tuna set types.
	S	5	"	3–8	4	"	0–13	
	P	1		0–3	1		0–6	
Dolphinfish	L	24*		18–31	27		0–50	Dolphinfish mainly with log–fish sets.
	S	7	"	5–10	7	"	0–26	
	P	2		1–4	3		0–23	
Yellowfin and skipjack tuna	L	66*	127	57–74	62	78/5	27–82	Skipjack common with school– and especially log–fish sets; seldom with porpoise–fish.
	S	40	266	34–46	45	225/10	8–63	
	P	3	392	1–6	2	325/12	0–8	

[1] Fleet sets are the data without T.M. Duffy sets; see text.
[2] Set types are log–fish (L), school–fish (S), and porpoise–fish (P) types.
[3] 95% CI of p's are from the binomial distribution. Trip fractions (n/T) are n sets from only those T trips having ≥10 sets. Asterisks indicate statistical significance among set types ($P \leq 0.05$).

which showed billfish significantly more frequent in log–fish sets (Fig. 3). Those rates ranged from 20% to 43% on different fishing trips. Sailfish *Istiophorus platypterus* comprised 31.4% of the billfish, the remainder being marlin. Several of the latter were identified as striped marlin *Tetrapturus audax* and black

Table 3

Fraction (p) of purse seine sets (n) having various associated "species," off Mexico (100–135°W).

		Fleet sets[1]						
		Overall fraction			Mean of trip fractions			
Associated spp.	Set type[2]	p (%)	n	95% CI[3]	p (%)	n/T	Range (%)[3]	Comments
Birds	L	—*	—	—	—	—	—	Birds very common with schools; virtually all porpoise–fish sets are with birds.
	S	77	104	68–85	72	80/4	50–100	
	P	98	220	93–100	98	169/6	91–100	
Sharks	L	—*		—	—		—	Sharks may be less frequent with school– than with porpoise–fish sets; cf. Table 2.
	S	6	"	2–12	3	"	0–11	
	P	13		7–21	14		0–43	
Rays	L	—		—	—		—	Rays similarly frequent with school– and porpoise–fish sets.
	S	9	"	4–16	8	"	0–18	
	P	5		2–11	5		0–8	
Billfish	L	—		—	—		—	Billfish relatively infrequent with both school– and porpoise–fish sets.
	S	4	"	1–10	5	"	0–9	
	P	3		1–8	5		0–23	
Bullet tuna	L	—		—	—		—	Rare in all set types.
	S	1	"	0–5	1	"	0–3	
	P	0		0–4	0		0–0	
Black skipjack	L	—		—	—		—	Not recorded.
	S	0	"	0–4	0	"	0–0	
	P	0		0–4	0		0–0	
Turtle	L	—		—	—		—	Relatively rare in all sets.
	S	3	"	0–8	1	"	0–3	
	P	3		0–8	4		0–9	
Dolphinfish	L	—*		—	—		—	Dolphinfish more often with school– than porpoise–fish sets.
	S	14	"	8–22	14	"	0–32	
	P	1		0–5	2		0–8	
Yellowfin and skipjack tuna	L	—*		—	—		—	Skipjack more often with school– than porpoise–fish sets; cf. Table 2.
	S	36	56	27–45	22	33/2	0–43	
	P	12	202	6–20	14	153/5	0–39	

[1] Fleet sets are the data without T.M. Duffy sets; see text.
[2] Set types are log–fish (L), school–fish (S), and porpoise–fish (P) types.
[3] 95% CI's are from the binomial distribution. Trip fractions (n/T) are n sets from only those T trips having ≥ 10 sets. Asterisks indicate statistical significance among set types ($P \leq 0.05$).

marlin *Makaira indica* (Table 4). The blue marlin *M. nigricans* was not present on the records examined, but occurs in the area. Usually 1 or 2 marlin were captured. Records of measured or estimated sizes show that some fish were large, e.g., a 3.2 m sailfish and a 4.4 m (total length) marlin. A swordfish *Xiphius gladius* was also recorded in one of the sampled sets.

"Bullet" tuna (*Auxis* sp.) and black skipjack *Euthynnus lineatus* are small tunas often taken in large numbers—but usually recorded in tons—in log–fish sets off Central America. Bullet tuna and black skipjack were very seldom in porpoise–fish sets. The association rate for bullet tuna was 10% for fleet log–fish sets and 41% for TMD log–fish sets (Table 2; Figs. 2, 3).

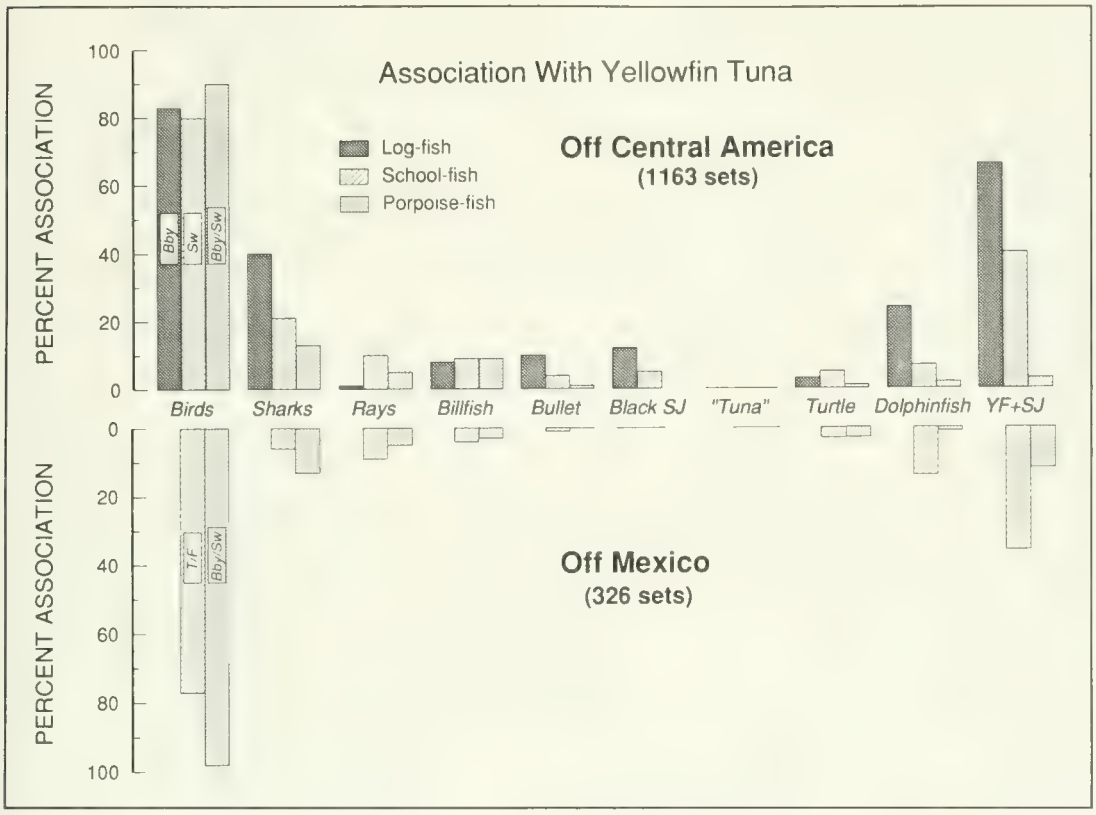

Figure 2
Percent association of different "species" with yellowfin tuna in fleet samples. Bby = boobies, Sw = shearwaters, T = terns, F = frigatebirds, "Tuna" = unspecified tuna species, YF = yellowfin tuna, SJ = skipjack tuna.

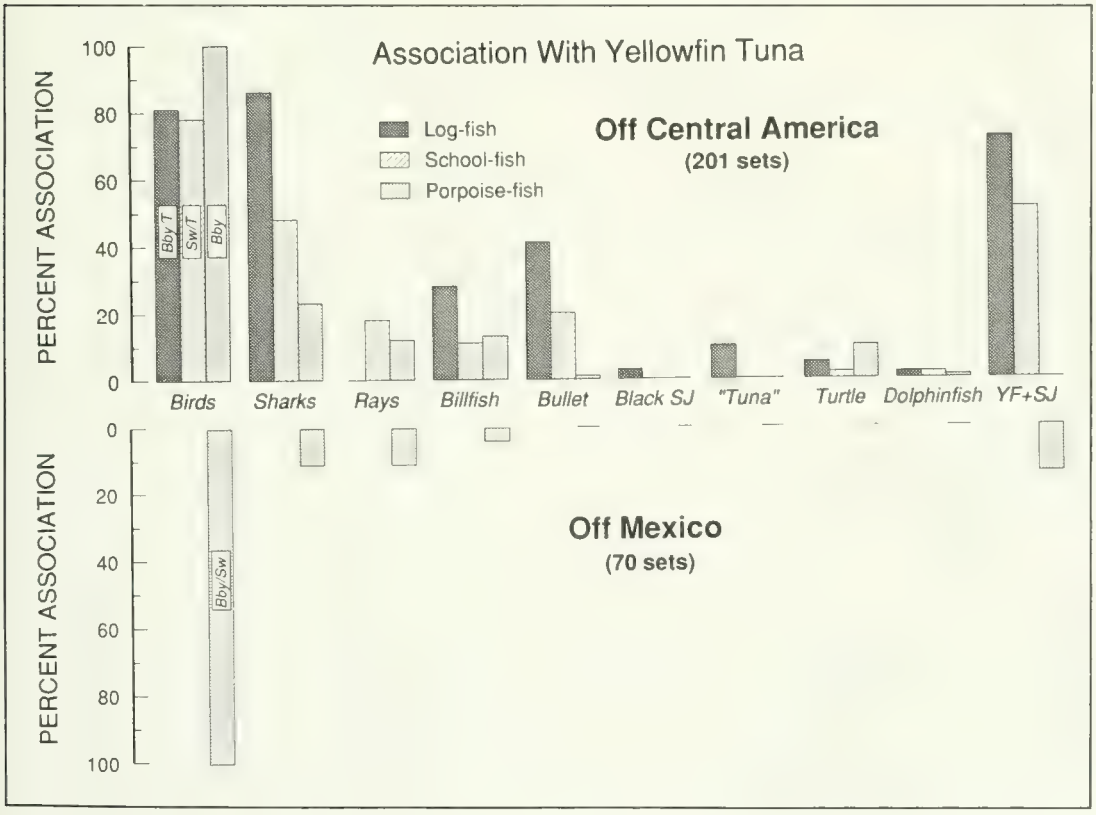

Figure 3
Percent association of different "species" with yellowfin tuna in T.M. Duffy samples. Bby = boobies, T = terns, Sw = shearwaters, "Tuna" = unspecified tuna species, YF = yellowfin tuna, SJ = skipjack tuna.

Table 4
Characteristics of tuna-associated species.

Species	Species[1] percent	Numbers of individuals/set[2] Mean	Range
Shark or "carcharhinid"	49.1	23.4	1–350
Silky (*Carcharhinus falciformis*)	25.2	29.2	1–500
Whitetip (*C. longimanus*)	9.0	5.1	1–39
Other carcharhinids (bull, "requiem," "brown," blacktip, gray)	6.1	11.6	1–80
Hammerhead (*Sphyrna* spp.)	3.9	2.3	1–7
Thresher (*Alopias* spp.)	3.2	3.6	1–28
Mackerel/Mako/White (Lamnidae)	2.4	8.3	1–40
Blue (*Prionace glauca*)	0.5	1.0	–
Whale (*Rhincodon typus*)	0.5	1.0	–
All (*N* 409)	(100.0)		
Ray	15.0	1.1	1–2
Manta (Mobulidae)	75.0	1.6	1–12
Others (Sting, bat, skate)	10.0	1.1	1–2
All (*N* 118)	(100.0)		
Swordfish (*Xiphias gladius*)	–	1.0	–
All (*N* 1)	(100.0)		
Billfish (Istiophoridae)			
Marlin (*Tetrapturus audax, Makaira indica*)	68.6	1.3	1–5
Sailfish (*Istiophorus platypterus*)	31.4	1.4	1–6
All (*N* 159)	(100.0)		
"Turtle" or Ridley (*Lepidochelys olivacea*)	87.5	1.4	1–4
Others (leatherneck, green)	12.5	2.5	1–3
All (*N* 24)	(100.0)		
Dolphinfish[3] (*Coryphaena hippurus*)	63.2	6.0	1–200
Amberjack/yellowtail (*Seriola* spp.)	30.5	11.8	1–100
Pompano (*Trachinotus*?, Kyphosidae?)	6.2	22.5	1–100
All (*N* 144)	(100.0)		
Wahoo (*Acanthocybium solandri*)	76.2	2.9	1–25
Spanish mackerel/mackerel (*Scomberomorus, Trachurus*?)	23.8	17.8	1–50
All (*N* 42)	(100.0)		
Ocean sunfish (*Mola mola*)	–	1.7	2–3
All (*N* 3)	(100.0)		

[1]From all data. Refers to species composition among individuals that could be identified or categorized.
[2]In sets that caught the species.
[3]Not including dolphinfish reported with other species absent.

Turtles were relatively infrequent in the tuna purse seine sets, at rates generally less than 5% overall and without evident pattern among the three set types. Most (21 of 24) were recorded as "turtle" or identified as Ridley turtles *Lepidochelys olivacea*, as probably most were (pers. observ.) (Table 4). A few leatherback turtles *Dermochelys coriacea* and green turtles *Chelonia mydas* were also identified.

Dolphinfish (*Coryphaena* spp.) were most frequent (24%) in log–fish sets and progressively rarer in school–fish and porpoise–fish sets. Individual fishing trips had log–fish sets with association rates ranging from zero to 50%. Considering that dolphinfish are frequently associated with flotsam and are not strong

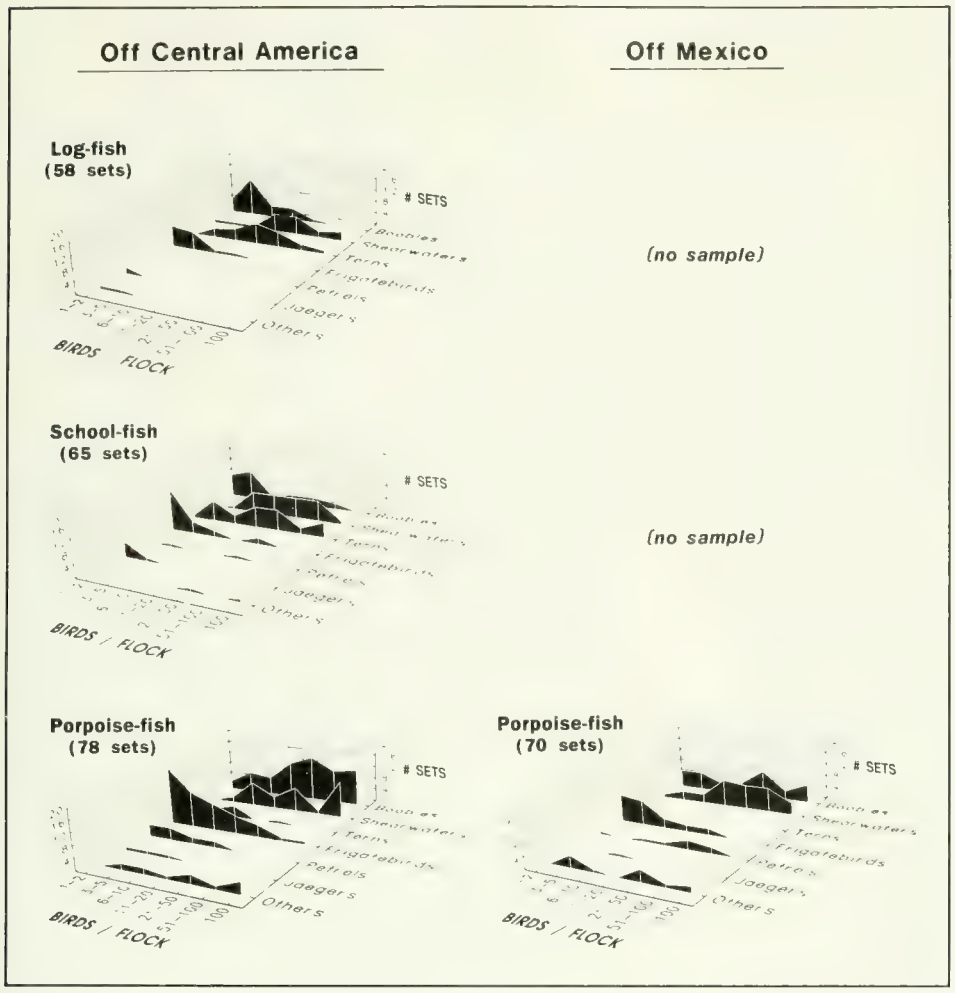

Figure 4
Histogram envelopes of bird flock sizes off Central America and off Mexico according to log–fish, school–fish, and porpoise–fish set types. Each histogram plots frequency (# SETS) against the species' abundance in the flocks (BIRDS/FLOCK). T.M. Duffy samples only.

swimmers like tuna, those trips with low occurrence rates may represent separation of this species from tuna during capture. When captured together with tuna, and with other associated fishes as well, dolphinfish averaged 6 individuals per set, with the range from 1 to 200 (Table 4).

Several other miscellaneous fishes were caught rather persistently, especially in log–fish sets. Notable among these were yellowtail or amberjack (*Seriola* sp.) and wahoo *Acanthocybium solandri* (Table 4). Others, such as triggerfish (Balistidae) were common and were probably associated with the flotsam near which the tuna were caught; these small fish are frequently seen under such objects (pers. observ.).

The fraction of successful (not total) purse seine sets that took both yellowfin and skipjack tuna measures the likelihood of these two tunas being associated. Yellowfin and skipjack were together in nearly 70% of successful log–fish sets. This fraction declined markedly in school-fish sets and even more so in the porpoise-fish sets, i.e., to 3% or less (Table 2).

The largest category of other animals associated with tuna was seabirds (Figs. 2, 3). Birds have a close relationship to tuna (and tuna fishing to birds), and observers usually record some aspect of their presence. Approximately 80% of log–fish and school–fish sets were in company with birds, and birds were present with virtually all porpoise–fish sets, regardless of area. The dominant bird species, as identified by the importance-ranking criterion, were usually boobies (*Sula* spp.) or boobies and shearwaters (*Puffinus* spp.) with log– and porpoise–fish sets; in the school–fish sets, the dominants were shearwaters or shearwaters and terns, *Sterna* especially (labeled histograms in Figures 2 and 3). The distribution of flock sizes of component species from the single-observer TMD data (Fig. 4) shows an increase in flocks and flock sizes of frigatebirds (*Fregata* spp.) and especially boobies in porpoise–fish sets relative to the other set types. Also, large tern flocks occurred primarily with school–fish sets. There was a shift toward larger shearwater flocks in the porpoise–fish sets off Mexico; the identifications

indicate these were wedge-tailed shearwaters *Puffinus pacificus*.

Discussion

As yellowfin tuna grow, they become involved in changing species associations, some of which are polyspecific in nature, i.e., like the associations studied elsewhere that seem situation-dependent, opportunistic, and often casual. This is reflected in the changing pattern in the association rates (p) from log–fish to school–fish to porpoise–fish sets on tuna; it is this pattern, rather than the actual rate values, that is of significance. The rates themselves should be used cautiously as they are derived from data affected by observer interest and from samples that were not large.

Foraging associates

Logs, or other floating objects, seem to provide opportune sites for development of species associations. Not only can logs attract prey and predators, but they can also drift to convergences where species gather. The behavior of predators feeding near flotsam is not simple, however. If the arrival rate of prey should decrease sufficiently, a passively feeding predator may switch to active, wide-ranging foraging (see Gerritsen 1984).

The very common association of sharks with tuna and the strong decrease in this association from log– to school– to porpoise–fish sets suggest that sharks mostly encounter tuna near flotsam. Then, like gray reef sharks (carcharhinidae) that follow feeding carangid fish for leftovers (Enewetak Is., pers. observ.), these sharks might follow the yellowfin as both scavengers and predators. Such behavior is probably of decreasing advantage as the tuna grow and forage more widely and at faster speeds. The tuna themselves, in some situations, may be attracted to sharks, as they are to whale sharks (Stretta and Slepoukha 1986).

The overall association rate for most other species with yellowfin tuna averaged in the 10% range, including that of billfish, rays, turtles, and smaller tunas. The marlins probably follow tuna both as parasitic foragers and as predators; they share many prey species with tunas and also eat tunas, especially the smaller specimens (see Shomura and Williams 1975). Unlike the sharks, however, these powerful fish appear to have little difficulty keeping up with fast-moving tuna; their association rates did not appear different among set types. Manta rays and turtles probably represent the opposite situation, where the tuna initiate and maintain the associations, perhaps as an extension of their proclivity to investigate flotsam. This may be why rays tended to be taken more often in the school–fish sets. The large schools of black skipjack, bullet, and skipjack tunas that are frequently taken with log-associated yellowfin may be obtaining feeding and protective advantages, but these benefits likely decrease as the yellowfin grow. The smallest tunas would find it increasingly difficult to swim at the speed of the yellowfin, and the danger of predation by the larger fish would also increase. It is first the black and bullet tunas that decrease in school–fish sets; finally even skipjack become scarce in the sets on the large, porpoise-associated yellowfin.

The most conspicuous and strong association with tuna is that of seabirds. Most bird species can feed independently of tuna, but they feed closely with these fish at every opportunity. The flocks of terns and smaller shearwaters that feed with free-swimming tuna of school–fish sets suggest that these fish of mainly nearshore waters feed on abundant, smaller prey. The larger, more mature tuna are farther offshore, feeding on sparser but evidently still-rich food patches. Dolphins and the larger seabirds, i.e., boobies and wedge-tailed shearwaters, feed with them (see also Au and Pitman 1986). The dominating importance of boobies in both porpoise–fish and log–fish sets suggests they forage by a wide and fast-ranging search for all discontinuities at the sea surface, including that of surface-schooling tuna and dolphins. Such foraging would be particularly effective offshore, for the yellowfin there have been found to prey more on fish (i.e., on larger but likely more patchily distributed prey) and less on crustaceans than do nearshore-caught yellowfin (Olson and Boggs 1986).

The porpoise–fish sets are themselves a category of species association, although not treated above as such. The highly mobile dolphins and the tuna of these sets appear to feed actively together; they share many of the same prey species (Perrin et al. 1973).

Enhanced foraging may be the main advantage of polyspecific associations involving the larger, more mobile species of tropical, pelagic seas; this may stem from converging foraging tactics among these animals. Just as boobies and shearwaters race about over a feeding tuna school to maximize interceptions of fleeting and unpredictably surfacing prey, yellowfin and other large species, on a larger scale, should range rapidly over large expanses to find sparse and unpredictable, yet relatively rich, prey patches. Food overlap would be increased by such nomadic foraging (see Huey and Pianka 1981), and strong patchiness of prey should itself reduce the tendency of each species to exploit different spatial intervals of the spectrum of prey distribution (see Terborgh and Stern 1987).

Polyspecific tuna and dolphins

The tuna–dolphin association of the ETP is the association most similar to the polyspecific associations studied among primates and terrestrial birds, in that specific species appear to forage together without strong or obvious interactions. However, virtually all porpoise–fish sets are attended by birds that appear to be closely following the feeding tuna (Au and Pitman 1986). That and the high 80–90% successful set ratio of these sets compared with the other set types (Table 1) suggest that dolphins do not commonly feed with birds that are not also with tuna. These specific dolphins that feed with tuna are ecologically successful (i.e., abundant, especially relative to other non-tuna-associated dolphin species; Au and Pitman 1988). And since these dolphins are largely found within the habitat of surface-schooling yellowfin in the ETP (see Allen 1985 for distributions), and not the converse, it could be that dolphins exploit the feeding behavior of tuna more often than the reverse. If so, this would agree with what seems typical in polyspecific associations, that it is the behaviorally more-adaptive species that takes advantage. Considering further the opportunistic, casual nature typical of polyspecific associations, one should not be surprised that tuna and dolphins are not intimately associated in many other seas and even in certain areas within the ETP. Moreover, if either the tuna or the dolphins were to be overexploited where they are associated, dire (or propitious) consequences to the other of the pair need not be expected.

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Parasite Fauna of Three Species of Antarctic Whales with Reference to Their Use as Potential Stock Indicators

Murray D. Dailey
Ocean Studies Institute, California State University
Long Beach, California 90840

Wolfgang K. Vogelbein
Virginia Institute of Marine Science
Gloucester Point, Virginia 23062

Abstract.–Seventeen species of parasites representing the Cestoda, Nematoda, Acanthocephala, and Crustacea are reported from three species of Antarctic whales. Thirty-five sei whales *Balaenoptera borealis*, 106 minke whales *B. acutorostrata*, and 35 sperm whales *Physeter catodon* were examined from latitudes 30° to 64°S, and between longitudes 106°E to 108°W, during the months of November to March 1976–77. Collection localities and regional helminth fauna diversity are plotted on distribution maps.

Antarctic host-parasite records from *B. borealis*, *B. acutorostrata*, and *P. catodon* are updated and tabulated by commercial whaling sectors.

The use of acanthocephalan parasites of the genus *Corynosoma* as potential Antarctic sperm whale stock indicators is discussed.

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The great whales of the southern hemisphere migrate annually between temperate breeding and Antarctic feeding grounds. However, results of Antarctic whale tagging programs (Brown 1971, 1974, 1978; Ivashin 1988) indicate that on the feeding grounds circumpolar movement by sperm and baleen whales is minimal. These whales apparently do not comprise homogeneous populations whose members mix freely throughout the entire Antarctic. Rather, each species appears to be comprised of functionally distinct breeding stocks, as demonstrated by the humpback whale *Megaptera novaeangliae*, which are isolated from one another by vast expanses of open ocean, large land masses, and geographically delimited feeding grounds (Klumov 1963, Mackintosh 1966, Gaskin 1976).

If commercial whaling is to resume at some future date (Marine Mammal Commission 1990), and if the whales are to survive, individual breeding stocks must continue to be managed throughout their entire range. Commercial quotas encompassing entire oceans are valid only if catch effort is proportionally spread across all stock units present in that ocean. In the past, economic considerations have resulted in concentration of fishing effort in localities where whales are most numerous and therefore easiest to find (Gaskin 1976). A direct result of this has been the successive overexploitation of several major whale species. To manage Antarctic whaling more effectively, identification and determination of whale stocks is of high priority (Schevill 1971, International Whaling Commission 1990).

The Antarctic whaling grounds were partitioned by the International Whaling Commission into commercial baleen and sperm whaling sectors (Fig. 1) based on the density distribution analyses of Hjort et al. (1932, 1933, 1935, 1938; as cited in Gaskin 1976). These sectors were thought to reflect whale stock distributions, and whaling quotas were previously allotted for individual sectors. Biochemical studies (Fujino 1960, 1964), morphometrics (Omura et al. 1970), scar density analyses (Shevchenko 1974), and marking studies (Brown 1979, Best and Butterworth 1980, Ivashin 1988) support these boundaries but indicate that more than one stock may occupy certain sectors. Definitive range limits are consequently still not known for most stocks of whales.

There is extensive scientific literature on the helminth fauna of Antarctic whales. However, the data have not been analyzed with respect to host distribution and stock identifica-

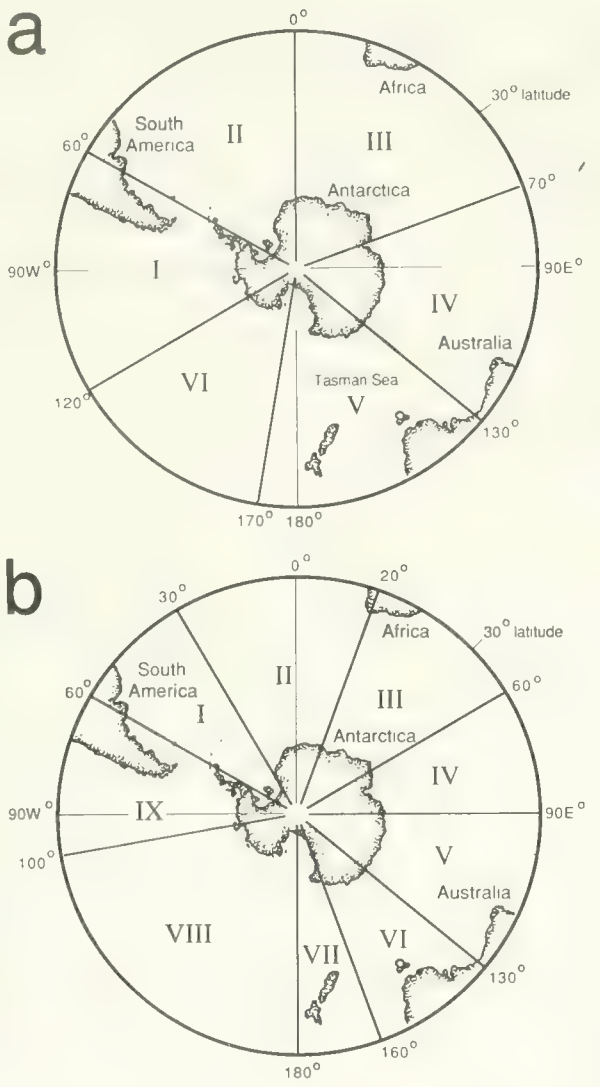

Figure 1
International Whaling Commission Antarctic commercial baleen (a) and sperm (b) whaling sectors.

tion. Reports have mostly discussed questions of helminth taxonomy or identified and cataloged the parasites. Klumov (1963) presented a zoogeographical analysis of the helminths of whales in the world oceans. Research on southern whales was begun by Russian helminthologists in 1963. In the course of two commercial voyages aboard the *Sovietskia Ukraina* and *Glory* during the 1963–64 and 1965–66 whaling seasons, 2164 marine mammals were necropsied; 2006 of these were whales. Due to the circumstances of commercial whaling, dissections were often incomplete with various organs being examined at varying degrees of thoroughness. The data obtained from this material were presented in a series of 22 papers from 1966 to 1975 (cited in Vogelbein 1981) and Skrjabin and Murav'eva (1978). Several British sources presented further data on cetacean helminths from various localities in the Antarctic Ocean (Prudhoe 1969, Markowski 1971, Gibson 1973, Gibson and Harris 1979).

The purpose of this paper is to report parasites from sperm, sei, and minke whales taken by two commercial vessels of the Japanese whaling fleet (1976–77). In addition, this paper will also update existing host-parasite lists, identify apparent variations in the zoogeographic distribution of helminths, and identify those helminths which are potential stock indicators.

Materials and methods

The data are obtained from two sources: Original materials collected by one of us (MDD) aboard the Japanese factory ships *Tonan Maru #2* and *Nisshan Maru #3* during November to March of the 1976–77 Japanese Antarctic whaling season, and Antarctic whale host-parasite literature records from 1915–89 (Vogelbein 1981, present study).

Baleen whales were captured in sectors I, IV, V, and VI (Fig. 1a); all sperm whales were captured in sector VIII (Fig. 1b). The length-frequencies and ages of the whales were not available to the authors. However, the catcher boats tend to take the largest animals possible during the harvest. Examinations of the external surface, blubber (subsample of ventral surface anterior to genital opening), organs (stomach, intestine, mesenteries, lungs, liver, kidneys, spleen, genitalia, placenta), blood, and fecal samples were carried out on a total of 176 whales, including 35 sei (*Balaenoptera borealis* Lesson, 1828), 106 minke (*Balaenoptera acutorostrata* Lacépede, 1804), and 35 sperm (*Physeter catodon* L., 1758). The helminths were prepared for identification using standard histological procedures (Dailey 1978). Voucher specimens are deposited at the Institute of Parasitology, California State University, Long Beach.

Results

Data collected during the 1976–77 Japanese Antarctic whaling season are presented in Tables 1 to 4 and Figures 2 and 3. A complete host-parasite record from all sectors for *B. borealis* and *P. catodon* is presented in Tables 5 and 6. Given the paucity of material reported from *B. acutorostrata* in Antarctic waters, a figure on parasites by sector has been omitted and only the information in Tables 1 and 3 represents this species. Several helminths are not identified beyond the generic level due to the condition of the specimens.

Table 1

Site of infection and percent infection rates for parasites of sei whale *Balaenoptera borealis*, minke whale *Balaenoptera acutorostrata*, and sperm whale *Physeter catodon* collected aboard Japanese whaling vessels during the 1976–77 Antarctic whaling season.

Parasites	Site of infection	Host species: *Balaenoptera borealis* (*N* 35)	*Balaenoptera acutorostrata* (*N* 106)	*Physeter catodon* (*N* 35)
Cestoda				
Cyclophyllidea				
Tetrabothrius				
T. wilsoni	intestine	40.0		2.7
T. affinis	intestine	11.4		
T. curilensis	intestine			2.7
T. sp.	intestine	57.1	7.5	
Priapocephalus				
P. grandis	intestine	5.7		2.7
Pseudophyllidea				
Diphyllobothrium				
D. sp.	intestine			2.7
Diplogonoporus				
D. balaenopterae	intestine	11.4		
Tetraphyllidea				
Phyllobothrium				
P. delphini	blubber			100
Monorygma				
M. grimaldii	mesenteries			5.7
Nematoda				
Ascaridoidea				
Anisakis				
A. physeteris	stomach			100
A. simplex	stomach	2.8		
A. sp.	stomach		0.94	
Habronematoidea				
Crassicauda				
C. crassicauda	penis	82.6 (*N* 23 males)		
Placentonema				
P. gigantissima	placenta			100 (*N* 2 with placentae)
Acanthocephala				
Polymorphida				
Bolbosoma				
B. turbinella	intestine	100		
B. physeteris	intestine			31.4
Corynosoma				
C. bullosum	intestine			5.7
Crustacea				
Cyamus				
C. balaenopterae	external		7.5	
Pennella				
P. balaenopterae	external	11.4	0.94	

Balaenoptera borealis

Nine helminth parasite species were found in sei whales captured in three commercial whaling sectors (Table 2). The mesoparasitic crustacean *Pennella balaenopterae* Koren and Danielssen, 1877 is also listed but is not included in the analysis. Two helminths occurred at very high prevalence. The acanthocephalan *Bolbosoma turbinella* (Diesing, 1851) infected all 35 hosts in high numbers. All sei whales were infected with cestodes of the genus *Tetrabothrius* Rudolphi, 1819. Two

Table 2

Parasite fauna of the sei whale *Balaenoptera borealis* from commercial whaling sectors I, V, and VI. (See Figure 2 for localities.)

	Locality	Date	*Tetrabothrius* *wilsoni*	*Tetrabothrius* *affinis*	*Tetrabothrius* sp.	*Priapocephalus grandis*	*Diplogonoporus balaenopterae*	*Anisakis simplex*	*Crassicauda crassicauda*	*Bolbosoma turbinella*	*Pennella balaenopterae*
		1976									
V (*N*10)	42°04′S 158°09′E	12-12	+	+			+		+	+	
	42°13′S 157°21′E	15-12			+		+			+	
	"	5-12	+							+	+
	41°29′S 160°06′E	17-12	+	+		+	+			+	
	42°15′S 158°09′E	18-12	+				+		+	+	
	44°22′S 153°39′E	25-12			+					+	
	43°41′S 156°06′E	26-12			+				+	+	
	"	26-12			+			+		+	+
	42°53′S 156°11′E	29-12			+				+	+	
		1977									
	46°22′S 173°01′W	6-01	+			+				+	
VI (*N*13)	48°24′S 153°48′W	15-01			+				+	+	
	50°00′S 144°00′W	19-01	+	+						+	
	55°00′S 141°00′W	21-01			+				+	+	
	56°34′S 140°58′W	25-01	+							+	
	58°41′S 148°50′W	27-01			+					+	
	"	27-01		+					+	+	
	59°28′S 155°47′W	29-01			+				+	+	
	"	29-01	+							+	
	"	29-01			+					+	+
	"	29-01	+							+	
	"	29-01			+				+	+	+
	53°24′S 149°20′W	1-02	+							+	
	54°00′W 145°49′W	2-02	+							+	
I (*N*12)	55°05′S 118°58′W	6-02			+				+	+	
	"	6-02	+							+	
	"	6-02	+						+	+	
	"	6-02			+				+	+	
	"	6-02			+				+	+	
	"	6-02			+				+	+	
	"	6-02			+				+	+	
	"	6-02			+				+	+	
	53°47′S 117°11′W	7-02	+						+	+	
	"	7-02			+					+	
	"	7-02			+				+	+	
	"	7-02			+				+	+	

Table 3

Parasite fauna of the minke whale *Balaenoptera acutorostrata* from commercial whaling sectors I, IV, and VI.

	Locality		Date	No. of whales	*Tetrabothrius* sp.	*Anisakis* sp.	*Cyamus balaenopterae*	*Pennella balaenopterae*
			1976					
IV	61°55′S	106°21′E	18-11	2			1	
(*N*51)	61°43′S	110°07′E	19-11	4	1		1	
	62°05′S	111°17′E	20-11	4				
	61°43′S	115°56′E	21-11	4				
	63°57′S	122°55′E	22-11	4				
	64°22′S	122°48′E	23-11	4	2			
	64°13′S	122°34′E	24-11	4				
	64°01′S	125°53′E	25-11	4				
	63°59′S	122°39′E	26-11	5				
	63°49′S	119°47′E	27-11	4				
	64°07′S	120°17′E	28-11	4				
	64°09′S	127°29′E	2-12	4				
	64°28′S	127°44′E	3-12	4				
			1977					
I	68°29′S	115°20′W	13-02	3				
(*N*40)	70°15′S	113°32′W	14-02	4				
	70°07′S	113°55′W	15-02	5	1		2	
	70°20′S	114°21′W	16-02	4			2	
	70°18′S	115°31′W	17-02	4				1
	70°01′S	114°57′W	18-02	4				
	70°54′S	112°12′W	19-02	3	1			
	70°19′S	110°08′W	20-02	4				
	69°58′S	108°15′W	21-02	5	1		2	
	70°34′S	113°57′W	22-02	4				
VI	70°45′S	121°21′W	23-02	3	1			
(*N*15)	70°44′S	124°36′W	24-02	2				
	70°55′S	123°11′W	25-02	10	1	1		

distinct species, *Tetrabothrius wilsoni* (Leiper et Atkinson, 1914) and *T. affinis* (Lönnberg, 1891; Lönnberg, 1892), and one form (*Tetrabothrius* sp.) that appears to fall between the two, comprised this tapeworm material (Table 1).

Helminth diversity appeared to be greater in the Tasman Sea (Sector V) animals than in whales captured on the open Pacific–Antarctic Ocean (Sectors I, VI) (Tables 2 and 5). Seven different helminths infected the sample of 10 sei whales from the Tasman Sea region of sector V. Only four helminths infected 13 whales from Pacific sector VI, while 12 whales from sector I were infected with only three species. The cestode *Diplogonoporus balaenopterae* Lönnberg, 1892 illustrates one disparity. This cestode infected 40% (Table 2) of the Tasman Sea sample yet it was absent in the other sectors. Likewise, the cestode *Priapocephalus grandis* Nybelin, 1922 and one nematode, *Anisakis simplex* Rudolphi, 1809, are seen only in sector V. *Tetrabothrius affinis* was found in sectors V and VI, and *T. wilsoni*, *Bolbosoma turbinella*, and

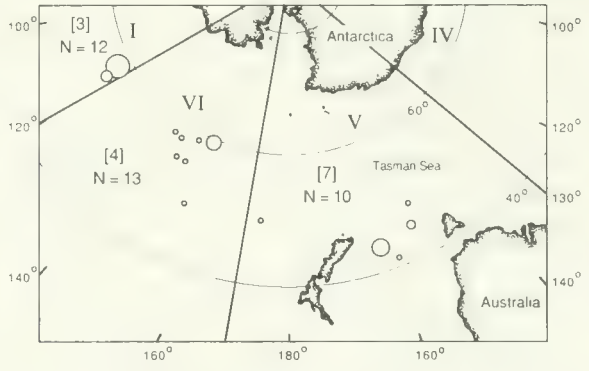

Figure 2

Location of 35 sei whale catches and number of helminth species found in IWC sectors I, IV, V, and VI. Circles indicate site of capture; circle size indicates relative number examined. Numbers in brackets are number of helminth species; *N* = number of whales examined.

Table 4

Parasite fauna of the sperm whale *Physeter catodon* from sector VIII. (See Figure 3 for localities and A, B, C, designations.)

	Locality	Date	*Tetrabothrius curilensis* (B)	*Tetrabothrius affinis* (B)	*Priapocephalus grandis* (C)	*Monorygma grimaldii* (C)	*Phyllobothrium delphini* (A)	*Diphyllobothrium* sp. (C)	*Anisakis physeteris* (A)	*Placentonema gigantissima* (C)	*Bolbosoma physeteris* (A)	*Corynosoma bullosum* (B)
		1977										
VIII	44°49′S 168°53′W	7-01					+		+		+	
	"	7-01					+		+			
	"	7-01	+				+	+				
	44°47′S 159°51′W	9-01					+		+			
	54°15′S 144°38′W	20-01					+		+			
	58°41′S 148°50′W	27-01		+			+		+		+	+
	54°56′S 151°41′W	31-01					+		+		+	
	64°35′S 116°44′W	12-02					+		+		+	+
	51°54′S 159°54′W	3-03					+		+		+	
	"	3-03					+		+			
	"	3-03					+		+			
	"	3-03					+		+			
	"	3-03					+		+		+	
	"	3-03					+		+			
	46°24′S 162°31′W	5-03					+		+			
	44°01′S 165°00′W	7-03					+		+		+	
	"	7-03					+		+		+	
	"	7-03					+		+			
	"	7-03					+		+			
	"	7-03					+		+			
	"	7-03					+		+			
	"	7-03					+		+			
	41°25′S 164°48′W	8-03					+		+			
	33°55′S 162°26′W	10-03					+		+			
	31°56′S 164°40′W	11-03			+		+		+		+	
	"	11-03					+		+			
	"	11-03					+		+			
	"	11-03					+		+			
	"	11-03					+		+			
	30°28′S 169°08′W	13-03				+	+		+		+	
	"	13-03					+		+		+	
	"	13-03				+	+		+			
	"	13-03					+	+	+			
	"	13-03					+		+	+		
	"	13-03					+		+	+		

Crassicauda crassicauda (Creplin, 1829) Leiper et Atkinson, 1914 were found in sei whales from all three sectors.

Balaenoptera acutorostrata

In comparison with the preceding host species, the parasite fauna of the minke whale are relatively poor.

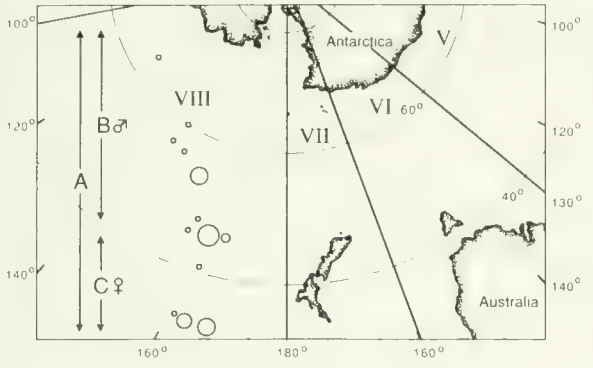

Figure 3

Helminth faunal diversity in 35 sperm whales from IWC sector VIII. Circles indicate site of capture; circle size indicates relative number examined. A = *Phyllobothrium delphini*, *Anisakis physeteris*, *Bolbosoma physeteris*. B = *Tetrabothrius curilensis*, *T. affinis*, *Corynosoma bullosum*. C = *Diphyllobothrium* sp., *Monorygma grimaldii*, *Placentonema gigantissima*, *Priapocephalus grandis*.

Four parasite species were found in 106 hosts captured in three whaling sectors (Table 3). The parasites included two helminths, *Tetrabothrius* sp. and *Anisakis* sp., and two parasitic crustaceans, *Pennella balaenopterae* and *Cyamus balaenopterae* Barnard, 1932. The ectoparasites are listed but not included in the analysis. A single female worm comprised the only *Anisakis* sp. infection. Since specific determination of adult anisakids requires examination of male specimens, this nematode was only identified to generic level.

Physeter catodon

Ten helminth species were recorded from 35 sperm whales (23 male, 12 female) captured in commercial sector VIII (Table 4). The larval cestode *Phyllobothrium delphini* (Bosc, 1802) and the nematode *Anisakis physeteris* Baylis, 1923 infected all sperm whale samples. The acanthocephalan *Bolbosoma physeteris* Gubanov, 1952, although infecting only 34.2% of the hosts, was found throughout the study area. Prevalence and intensity of infections for the remaining helminths were low and geographical distributions were restricted.

Figure 3 illustrates a latitudinal disparity in the helminth fauna of sperm whales from sector VIII. Group A represents three helminths (*P. delphini*, *A. physeteris*, *B. physeteris*) common in sperm whales throughout the study area. Group B comprises three helminths (*Tetrabothrius curilensis* (Gubanov, 1952), *T. affinis*, and *Corynosoma bullosum* (Linstow, 1892))

Table 5

Summary of the helminthological fauna of the sei whale *Balaenoptera borealis* reported for all six Antarctic whaling sectors (Vogelbein 1981; present study).

	Whaling sector					
Parasite	I	II	III	IV	V	VI
Cestoda						
Tetrabothrius affinis		+	+		+	+
Tetrabothrius wilsoni	+	+	+	+	+	+
Tetrobothrius sp.	+				+	+
Priapocephalus grandis		+			+	
Diplogonoporus balaenopterae		+	+		+	
Diphyllobothrium sp.		+				
Phyllobothrium delphini					+	
Acanthocephala						
Bolbosoma turbinella	+	+	+	+	+	+
Bolbosoma tuberculata		+				
Bolbosoma balaena				+	+	
Nematoda						
Crassicauda crassicauda	+				+	+
Crassicauda delamureana		+	+			
Crassicauda sp.		+				
Anisakis simplex		+			+	+
Anisakis sp.		+				
Trematoda						
Ogmogaster plicatus		+				
Ogmogaster antarcticus	+				+	
Lecithodesmus goliath		+				

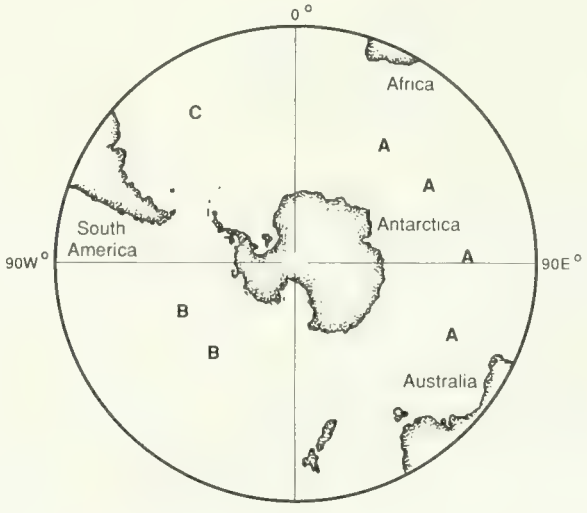

Figure 4

Distribution of acanthocephalans of the genus *Corynosoma* in Antarctic sperm whales. A = *C. mirabilis*; B = *C. bullosum*; C = *C. singularis*.

Table 6
Summary of the helminthological fauna of the sperm whale *Physeter catodon* reported for all nine Antarctic whaling sectors (Vogelbein 1981; present study).

	Whaling sector								
Parasite	I	II	III	IV	V	VI	VII	VIII	IX
Cestoda									
Diphyllobothrium sp.								+	
Tetrabothrius affinis	+		+					+	+
Tetrabothrius wilsoni							+		
Tetrabothrius curilensis								+	
Priapocephalus grandis		+					+	+	
Priapocephalus sp.								+	
Polygonoporus giganticus					+				
Multiductus physeteris								+	
Phyllobothrium delphini	+	+	+	+	+	+	+	+	+
Monorygma grimaldii								+	+
Tetraphyllidea sp.	+							+	+
Acanthocephala									
Bolbosoma physeteris								+	
Bolbosoma tuberculata				+					
Bolbosoma sp.		+							
Corynosoma singularis	+								
Corynosoma mirabilis			+	+	+				
Corynosoma bullosum								+	
Nematoda									
Anisakis physeteris	+	+	+	+				+	
Anisakis catadontis		+							
Anisakis simplex		+							
Placentonema gigantissima								+	+
Placentonema sp.									+

found only in large bulls from the higher latitudes. Group C comprises four helminths (*P. grandis*, *Monorygma grimaldii* (Moniez, 1889) Baylis, 1919, *Diphyllobothrium* sp., and *Placentonema gigantissima* Gubanov, 1951) found only in female whales captured in the lower latitudes.

Discussion

The prediction that, "When a species of host is divided into two or more population groups separated geographically in different environments, their respective parasite faunas will exhibit differences" (Noble and Noble 1964) is particularly true for helminths that generally require more than one host to complete their life history. The occurrence of a particular parasite in any geographic locality depends upon the presence of a suitable definitive host, suitable intermediate host(s), and complex biological factors which impart a strict interdependency on the organisms comprising the host-parasite complex.

Knowledge of host dietary composition is very important in studying cetacean helminth zoogeography. Over any area as large as the Antarctic Ocean, widely separated stocks of whales may exploit different food organisms.

Kawamura's (1974) report on the feeding ecology of southern hemisphere sei whales recognized a latitudinal succession of major food species. In its southward migration, the sei whale exploits several major food organisms: euphausiids at high latitudes, pelagic amphipods at low latitudes, and copepods at intermediate latitudes (Gaskin 1982). Kawamura (1974) also recognized longitudinal variations in the availability of prey species. Euphausiid crustaceans comprise the bulk of this host's diet in sectors IV through VI while amphipods are more prevalent in their diet in sectors III and IV. Calanoid copepods are of considerable supplementary importance in sectors V and VI. As a species, the sei whale is the most euryphagous balaenopterid whale (Klumov 1963). Budylenko (1978) lists over 80 prey species for this host. Yet Kawamura (1974) indicates that individual sei whales are stenophagous feeders, where stomachs containing more than one prey species are rare.

Since the prey species are, in all probability, the intermediate hosts of cetacean helminths, variable dietary compositions within species of whales will manifest themselves in their respective helminth faunas. Thus, individual stocks of whales may be distinguishable by regional helminthofaunal peculiarities.

Seventeen species of helminth have been reported from the sei whale (Table 5). Two of these helminths, the acanthocephalan *Bolbosoma turbinella* and cestodes of the genus *Tetrabothrius*, were found in all sei whales sampled in the 1976–77 season. Skrjabin (1968) also found a very high prevalence and intensity of these worms in sei whales throughout the Antarctic.

The tetrabothriids obtained from sei whales in 1976–77 represent two distinct species and one ambiguous form (Table 2). Two (*T. wilsoni*, *T.* sp.) have a very high prevalence of infection and the other (*T. affinis*) occurs less frequently.

The remaining helminths are encountered less frequently in sei whales and several have a very restricted geographical distribution (Table 5). Skrjabin (1975) reported several helminth species whose distributions were limited to specific geographical localities. He

recorded the nematode *Anisakis simplex* only from sei whales of the "Notalia Zone" (northern boundaries of whaling sectors). Another nematode, *Crassicauda delamureana* Skrjabin, 1966, was reported only in the "Notalia Zone" of sectors II and III; the acanthocephalan *Bolbosoma tuberculata* Skrjabin, 1970 only in the South Atlantic; *Bolbosoma balaenae* (Gmelin, 1970) only in sectors IV and V; and the trematode *Lecithodesmus goliath* (van Beneden, 1858; Braun, 1902) was confined to the southeast coast of South America. The trematode *Ogmogaster antarcticus* Johnston, 1931 was recorded only from sectors I and V, while the larval cestode *P. delphini* parasitized sei whales only in sector V, south of New Zealand. Although prevalences of infection are low in all of the above cases, as more information is gathered these helminths may help to identify local, isolated stocks of whales.

Other helminths such as the cestodes *T. affinis* and *P. grandis* have a limited geographical distribution in sei whales, but the fact that these species are polyxenous extends their known range significantly. These helminths are consequently of limited potential value in identifying sei whale stocks.

Differences in the helminthofaunal diversity are evident between three host stocks captured in sectors V, VI, and I during 1976–77 (Fig. 2). It is probable that regions of upwelling in the coastal waters of New Zealand and Australia provide sufficient nutrients to support a greater diversity of free-living organisms than would be expected in the open Pacific Ocean. Consequently, a greater diversity of prey species (hence intermediate hosts) is likely to be exploited in the coastal waters, inflicting these sei whale stocks with a higher diversity of helminths.

The helminth fauna of the Antarctic minke whale has been poorly studied. The only prior investigation is that of Skrjabin (1975) who examined six hosts from the Balleny Island region (sector V) and sector IV, and found them uninfected. Our study is the first to examine a large number of Antarctic minke whales. The number of helminths found infecting this host was very few (Tables 1, 3). The only significant infection is that of *Tetrabothrius* sp. With this limited information available, Antarctic stocks are presently indistinguishable with respect to their helminth fauna.

Skrjabin (1975) believes that this poor helminth fauna is due to the minke whales' feeding habits. The diet of the southern minke whale is more restricted than that of other Antarctic whales. Ohsumi et al. (1970) reported that most minke whales congregate south of the Antarctic Convergence and feed almost exclusively on *Euphasia superba*. Stomach samples occasionally contained small amounts of other prey species. This host penetrates the furthest south of all the whales and inhabits the ice pack close to the Antarctic continent. It feeds almost exclusively on *E. superba* which are not found to be infected with larval helminths (Kagei 1974, Kagei et al. 1978).

The known helminth fauna of the sperm whale is presently comprised of 18 species (Table 6) which may be subdivided into several distinct components. Two helminths, the larval cestode *Phyllobothrium delphini*, and the stomach nematode *Anisakis physeteris*, occur at very high prevalence and intensity throughout the Antarctic. Since these parasites have a cosmopolitan distribution in odontocetes, they are probably useless in distinguishing between southern sperm whale stocks in the longitudinally defined IWC sectors of the Antarctic. However, *P. delphini* may be important from a latitudinal aspect. For example, Walker (1987) found latitudinal differences in the occurrence of this parasite in Dall's porpoise *Phocenoides dalli* True, 1885 taken in the northern North Pacific and Bering Sea. The absence of *P. delphini* in *B. acutorostrata* and the very low frequency of occurrence in *B. borealis* along with its ubiquitous occurrence in the sperm whale tend to substantiate the more pronounced seasonal north–south movement of the Antarctic sperm whale stock(s) into temperate waters. Best (1974), Gambell (1972), and Gaskin (1971) all report extensive migrations ranging from tropical latitudes (north of 35°S) to above 60°S for males forming "bachelor" herds. Best (1974) calculated from mark returns that the average annual movement was approximately 850 nautical miles (1410km) for males, and 372 (620km) for females.

Acanthocephalans belonging to the genus *Corynosoma* may, however, be of some value in distinguishing the Indian Ocean–Antarctic stocks of sperm whales from those in the Atlantic and Pacific–Antarctic (Fig. 4). *Corynosoma mirabilis* was found in 18 large male sperm whales from Africa to Australia (sectors III, IV, and V) in the Indian Ocean. This species was found only between 40° and 60°S latitude. In the 1976–77 material, whales taken in the southern portion of sector VIII were infected with immature *C. bullosum*. Sexually immature *Corynosoma singularis* are reported from a single sperm whale captured in the southwestern Atlantic Ocean (sector I) (Skrjabin 1971) and also as adults in a leopard seal from the Balleny Islands. Despite the fact that these acanthocephalans attain sexual maturity only in the Phocidae, these larval forms in the sperm whale may have the possibility of serving as regional stock indicators.

Local variations in the helminth diversity of sperm whales captured in sector VIII during 1976–77 are illustrated in Figure 3. Variable infections are noted between male and female sperm whales. It is difficult to say whether these distributional peculiarities are coincidental or real due to small sample sizes. Assuming that they are real, they become very difficult to

interpret. *Tetrabothrius curilensis* and *T. affinis*, although recovered only from the higher latitudes in this sample, may have been carried south by migrating whales. *Tetrabothrius affinis* has previously been recorded from lower latitudes in other host species. *Corynosoma bullosum*, on the basis of the previous discussion, may be characteristic of the high-latitude feeding grounds. This helminth matures in pinnipeds from the Balleny Islands and the Antarctic coast. *Monorygma grimaldii* has thus far been reported only from the lower latitudes, and *Placentonema gigantissima* may also be restricted to temperate waters. To date, *P. gigantissima* has only been found in female whales which do not penetrate as far south as the males.

In his commentary on the case for scientific whaling, Nagasaki (1990) states, "Our ignorance about the biology of whales is delaying any informed discussion about the practice of commercial whaling." He goes on to discuss Japan's recent scientific whaling program. The data presented in this study on the parasitic fauna found in these Antarctic whales is just one more piece of information that can help the scientific community understand the Antarctic ecosystems and, hopefully, with it, improve our ability to better assess the status of Antarctic whale stocks.

Acknowledgments

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Detecting Trends in Harbor Porpoise Abundance from Aerial Surveys Using Analysis of Covariance

Karin A. Forney
La Jolla Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, California 92038

Doyle A. Hanan
California Department of Fish and Game, c/o Southwest Fisheries Science Center
La Jolla Laboratory, National Marine Fisheries Service, NOAA
P.O. Box 271, La Jolla, California 92038

Jay Barlow
La Jolla Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, California 92038

Abstract.– Aerial surveys designed to detect trends in the abundance of harbor porpoise *Phocoena phocoena* were conducted each autumn, 1986 through 1990. The number of porpoise seen per kilometer of survey effort was used as an index of abundance. Based on these surveys, an analysis of covariance was used to model porpoise abundance. Year was treated as a covariate, and factors which affected sighting rates were included as categorical variables. No significant changes were seen in the abundance of porpoise over the five survey years. Monte Carlo simulations were performed to determine the power of the ANCOVA to detect trends in abundance. We conclude that the ability to detect trends is poor if traditional levels of statistical significance ($\alpha = 0.05$) are used. A larger α-error may be appropriate in the management context of this species and increases the power to detect trends. Additional survey years similarly improve the power to detect trends. Based on the results of the simulations, we suggest that power should be defined to include only the detection of the correct trend when two-tailed tests are employed.

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Harbor porpoise *Phocoena phocoena* are caught incidentally during halibut fishing with gillnets along the central California coast (Diamond and Hanan 1986; Hanan et al. 1986, 1987; Barlow 1987; Barlow and Hanan 1990). To assess the potential impact of this fishery mortality, ship and aerial surveys have been used to estimate the abundance of harbor porpoise along the coast of California, Oregon, and Washington (Barlow 1988, Barlow et al. 1988). These authors showed that although aircraft can be used to survey a large area very quickly, abundance estimates from aerial surveys must be multiplied by a very large and uncertain correction factor to account for the majority of animals that will be underwater at any given instant. For this reason, ship surveys were concluded to be preferable for estimating absolute porpoise abundance.

The requirements are, however, less stringent if the only goal is to detect trends in the abundance of porpoise over time, rather than determining absolute abundance. The ability of aircraft to cover great distances relatively quickly and inexpensively makes them a logical platform for such surveys. If the fraction of animals detected from the air does not change over time, the correction factor becomes irrelevant, and indices of relative abundance can be used in place of absolute abundance measures.

We describe a series of five aerial surveys for harbor porpoise conducted in central California during autumn of 1986, 1987, 1988, 1989, and 1990. These surveys were designed specifically to detect changes in porpoise abundance. We used twin-engine aircraft to fly predetermined transect lines which zigzagged up the coast between Point Conception and the mouth of the Russian River (Fig. 1). Line transect methods were used with one observer on each side of the aircraft and a belly-port observer. A fourth person recorded information pertaining to sightings of porpoises and sighting conditions. Each year within the survey period, the transect lines were repeated 3–7 times, depending on weather conditions.

The number of porpoise seen per kilometer of search effort was used as a measure of relative abundance. A stepwise analysis of covariance procedure (ANCOVA) with year as the covariate was used to identify the best model describing porpoise seen

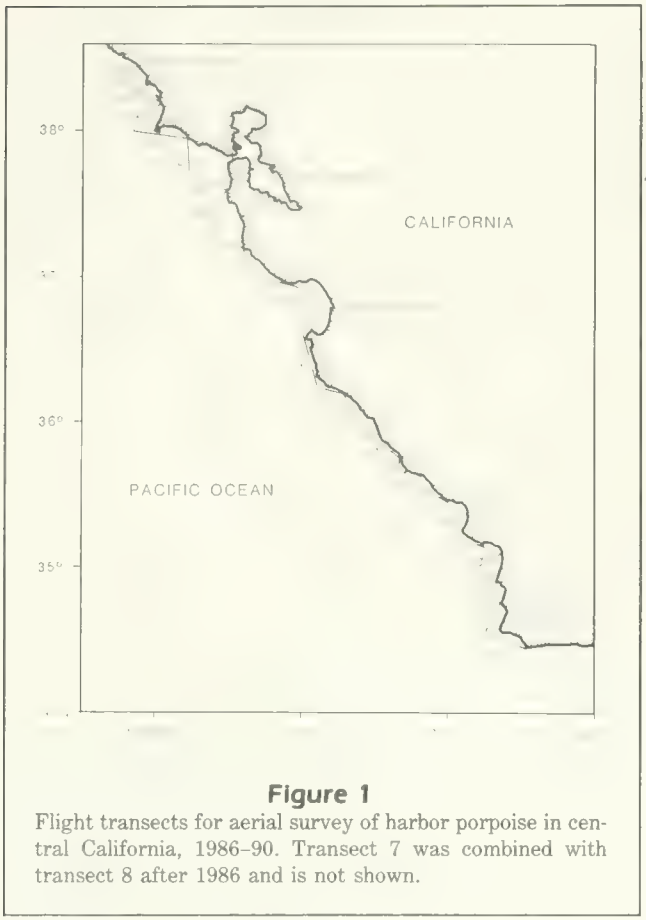

Figure 1
Flight transects for aerial survey of harbor porpoise in central California, 1986–90. Transect 7 was combined with transect 8 after 1986 and is not shown.

per kilometer. Standard ANCOVA F-ratio tests were applied to determine whether a significant trend with year is present. Monte Carlo methods were used to determine the power of this test to detect known trends in abundance.

Methods

Field methods

The surveys were established to monitor changes in abundance within the range of porpoise/gillnet fishery interactions (Point Conception to Russian River, California). Surveys were started only when there was a good likelihood of completing at least half of the survey (Point Conception to Monterey, or Monterey to Russian River) under good weather conditions. They were halted when viewing conditions deteriorated below acceptable levels (sea state higher than Beaufort 4 or 5, excessive dark cloud cover, rain, or fog).

A series of predetermined locations marking the beginning and end of each transect was entered into the aircraft's LORAN C navigational receiver to give the pilot a course to follow. The transects zigzagged in a generally northward progression between shore and roughly the 50-fathom (91-m) contour (Fig. 1). Sightings at the endpoint of a transect were very rare, and duplication at the start of the next transect did not occur. The transect lengths ranged from 5.2 to 44.8 km and averaged 24.8 km. The aircraft maintained an altitude of approximately 213 m and speeds of 90–100 knots (167–185 km/hour). To reduce sun glare, surveys were conducted only from south to north.

The surveys were flown in a twin-engine, high-wing, seven-passenger aircraft with the rear seat removed (Partenavia P68). Two observers sat behind the pilot and copilot seats and looked out the side windows; a third observer (belly observer) lay on the floor on his/her stomach just behind the right-side observer's seat and surveyed the water below the airplane through a 25 × 30-cm rectangular viewing port. Starting in 1988, the side windows were fitted with plexiglas bubble-type windows, allowing the side observers to see from the horizon to directly under the plane. This created an overlap with the belly observer's field of view; however, this did not result in double counting because the observers were in constant communication and discussed all possible sighting duplicates as they occurred.

The data recorder sat in the copilot position and recorded flight information, including location (latitude and longitude), time, weather (% cloud cover, Beaufort sea state, and sun position), viewing conditions, and porpoise sighting information. The data recorder entered weather and viewing conditions at the start of each transect and whenever conditions changed. Each observer subjectively evaluated viewing conditions as excellent, good, poor or "off effort," depending on estimated viewing depth into the water, sun glare, and sea state. To simplify the recording procedure and enhance accuracy of the data, a lap-top computer connected to the LORAN C navigational receiver replaced the hand-written flight log during the 1988–90 surveys.

The pilot, recorder, and observers communicated through headsets and voice-activated microphones. All communication was recorded on a central tape recorder. Additionally, each observer used a hand-held tape recorder for storage of individual sighting information. The two side observers used hand-held inclinometers to measure declination angles in degrees to the animals sighted. Due to space limitations, the belly observer could not use an inclinometer and estimated angles using marks applied to the viewing port. The observers changed positions approximately every 1–1.5 hours and between flights.

The observers actively searched (were "on effort") from start to finish of a transect, except when circling or when they declared themselves "off effort" because

of poor sighting conditions. The pilot circled on porpoise sightings if there was any question about species identification or number of porpoise. Additional sightings made while circling were recorded as "off effort" sightings and were not included in the analyses.

During the first survey year (1986), observers reported all marine mammals sighted. However, the large number of California sea lion sightings took a disproportionate amount of time, so only harbor porpoise were recorded in 1987–90. Following the surveys, the data in the flight log or computer were checked for accuracy and, if needed, compared with the tape recordings. The data were transferred into microcomputer databases for summary and analysis.

Analytical methods

Individual flight segments during which all sighting conditions were constant were combined to measure porpoise per kilometer in relation to each of the sighting variables. These variables included Beaufort sea state, cloud cover, viewing condition, individual observers, and an *a posteriori* geographic subdivision chosen on the basis of apparent porpoise abundance: south (low abundance) and north (high abundance) (Fig. 2). This subdivision was created to correct for slight interannual differences in survey effort for high- and low-density areas, caused by bad weather.

Cloud cover was recorded as a percentage and later coded into the categories "clear" (0–24%) and "cloudy" (25–100%). Sighting efficiency and sample sizes decreased dramatically when Beaufort sea state was higher than 3, so only segments with Beaufort 0–3 were used. Beaufort 0 was combined with Beaufort 1 because there was very little survey effort at Beaufort 0.

The data were fitted to an analysis of covariance (ANCOVA) model of the form:

$$P = \mu + \alpha_1 + \alpha_2 + \ldots + \delta(y - \bar{y}) + \varepsilon \qquad (1)$$

where P represents the log-transformed ($\log_e$) value of porpoise per kilometer, μ is the mean value of P, the α represent qualitative factors influencing observed porpoise abundance, δ represents the coefficient for the covariate year (y), $\bar{y}$ is the mean value of y, and ε is a random error term. Such an additive model for logarithmic values is equivalent to a model describing multiplicative effects on the untransformed number of porpoise seen. This was deemed appropriate because sighting conditions affect the fraction of porpoise seen but not the absolute density of porpoise present. Because of the logarithmic transformation, a linear

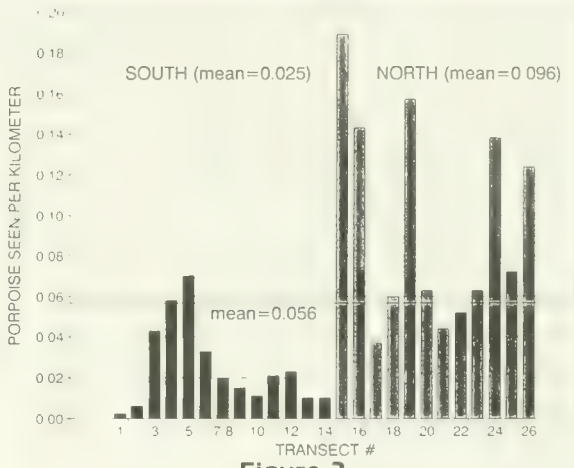

Figure 2

Porpoise seen per kilometer in transects 1 through 26 for 1986–90 surveys (including Beaufort sea states 0–3 and clear skies only). For the analysis, transects were divided into two areas at Point Pinos (between transects 14 and 15): south (low abundance) and north (high abundance).

increase or decrease in the covariate would be interpreted as an exponential increase or decrease in porpoise abundance. The constant 0.001 was added to each value before transformation to avoid trying to take the logarithm of zero. This logarithmic transformation also made the data more nearly normal (Fig. 3).

It was not possible to include all potential variables in the model selection procedure, because this would have caused overstratification of the data. Individual observer effects were excluded because not all observers collected data each year, resulting in a large number of missing cell values. Viewing condition was also excluded because it is somewhat redundant with sea state and cloud cover and it is more subjective. Previous nonparametric tests of individual observer effects and viewing conditions with three years of data (Forney et al. 1989) yielded no significant differences in observed numbers of porpoise per kilometer.

In the ANCOVA, the data were weighted by the number of kilometers flown to correct for variability due to unequal sample sizes. A stepwise selection procedure with the SAS procedure GLM (Joyner 1985) was used to determine the best model for the observed data. At each step, all appropriate parameters and interaction effects were tested individually. The most significant parameter was added to the model, based on a criterion level of $\alpha = 0.05$. Each included variable was retested for significance at each subsequent step of the procedure.

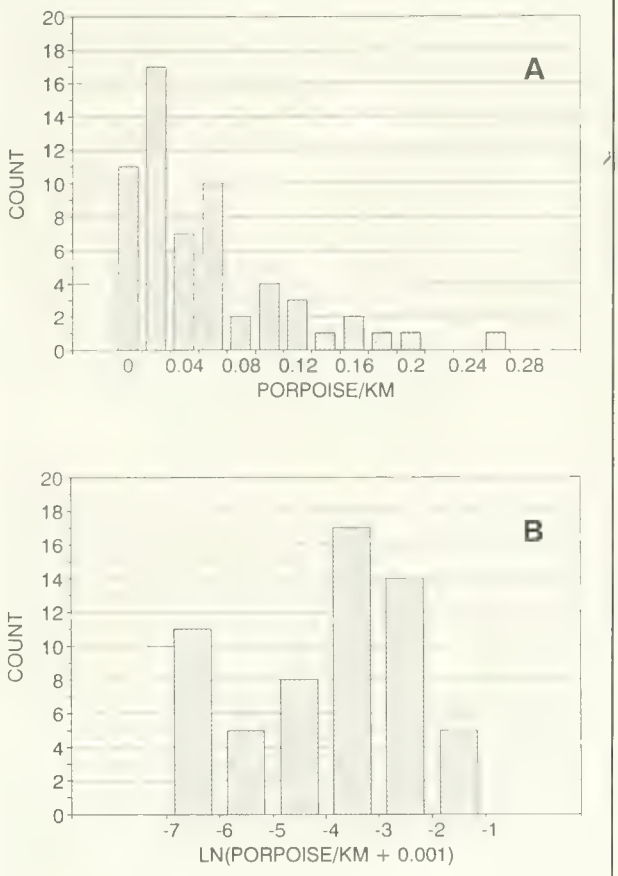

Figure 3

Distribution of observed porpoise/km values (A), and log-transformed porpoise/km values (B) for five years of aerial survey data. The transformation was ln(x + 0.001), where x is the observed number of porpoise/km.

Table 1

Average number of harbor porpoise seen per kilometer of search effort for 1986–90 aerial surveys. Numbers of porpoise seen per number of kilometers surveyed are given in parentheses. Categories are defined in the text. Overall mean number of porpoise per kilometer is 0.047 (796/16948).

Area	Cloud cover	Beaufort 0, 1	Beaufort 2	Beaufort 3
South	Clear	0.036 (75/2075)	0.024 (54/2248)	0.013 (24/1918)
	Cloudy	0.030 (31/1026)	0.015 (15/974)	0.006 (3/518)
North	Clear	0.163 (170/1042)	0.106 (229/2165)	0.046 (84/1814)
	Cloudy	0.058 (30/521)	0.039 (59/1530)	0.020 (22/1117)

Simulation methods

Once the best model had been selected (see Results), Monte Carlo simulations were performed to determine the power of the ANCOVA to correctly detect a given trend in porpoise abundance. The analysis of power was divided into two main steps: (1) Simulations without a trend, to determine whether the procedure can create and correctly analyze simulated data; and (2) simulations with trends, to estimate how often the procedure correctly identifies a known trend in harbor porpoise abundance. Annual changes of ±5% and ±10% were tested over periods of five, six, eight, and ten years.

The random data sets were generated using the parameters and error structure obtained for the actual data from the best model (see Results). First, the expected logarithmic value of porpoise per kilometer for each combination of conditions was calculated from the fitted parameters. A random error term for each expected value was then drawn from a normal distribution with a mean of zero and standard error from the ANCOVA results of the best model. To allow weighted analysis of the simulated data, this error term was weighted inversely, i.e., multiplied times $\sqrt{(1/w)}$, where w is the number of kilometers flown under the given conditions. A set of 60 values for w, one for each of the 60 simulated porpoise-per-kilometer values, was obtained for each year by randomly selecting the actual numbers of kilometers flown from one of the five survey years. Complete yearly sets were chosen rather than individual values to avoid unlikely combinations of kilometers flown.

A yearly trend was incorporated into the simulation data by multiplying the calculated value of porpoise per kilometer times a factor representing the desired exponential change in porpoise abundance. To make the simulated data more like potential real data, all values were rounded to yield only integer values of porpoise over the given number of kilometers flown. In addition, to prevent unfeasible values of porpoise per kilometer, a new error term was drawn if the original one resulted in a value which was negative or greater than 0.4 porpoise per kilometer. The highest value observed in 1986–90 was 0.24 porpoise per kilometer; multiplying this value times the maximum simulated increasing trend yields an upper limit of approximately 0.4 porpoise per kilometer. Less than 5% of all error terms were redrawn in the simulations.

Table 2

Stepwise model selection procedure for 1986–90 aerial survey data. Parameters marked with an asterisk indicate variables included in the model at each step. P = ln(porpoise/km + 0.001); μ = mean value of P; BF = Beaufort sea state; AR = area; CL = cloud cover; YR = year; an × between letters indicates an interaction effect.

STEP	1	2	3	4
Base model	$P = \mu$	$P = \mu + AR$	$P = \mu + AR + CL$	$P = \mu + AR + CL + BF$
P-values for tested variables	BF: 0.0587	BF: 0.0079	*BF: 0.0016	YR: 0.8535
	*AR: 0.0001	*CL: 0.0021	YR: 0.5865	BF×AR: 0.8491
	CL: 0.0256	YR: 0.9628	CL×AR: 0.3399	BF×CL: 0.8378
	YR: 0.9258			CL×AR: 0.3875

Results

Survey results

A total of 16,948km of survey effort during 1986–90 resulted in 431 sightings, representing a total of 796 harbor porpoise. The overall mean number of porpoise per kilometer was 0.047. The average values of porpoise per kilometer over the five years are listed in Table 1 for different sighting conditions and areas. Mean group size was 1.85 porpoise, with a range of 1–10 and median 1.

The model

The following model provided the best fit to the observed logarithmic estimates of porpoise per kilometer:

$$P = \mu + \alpha_{Bi} + \alpha_{Cj} + \alpha_{Ak} + \varepsilon_{i,j,k} \qquad (2)$$

where P = $\log_e$ of [(porpoise/km) + 0.001],
μ = mean value of P,
α_{Bi} = effect of Beaufort sea state i on P,
α_{Cj} = effect of cloud cover j on P,
α_{Ak} = effect of area k on P,
$\varepsilon_{i,j,k}$ = normally distributed error with a mean of zero.

The model selection procedure is outlined in Table 2. None of the included variables lost significance and subsequently had to be dropped after inclusion of other variables. The yearly trend was not significant, so the model is essentially reduced to an analysis of variance (ANOVA) model. The results of the complete ANCOVA model testing for a yearly trend in the 1986–90 harbor porpoise data are shown in Table 3. The effects of area, cloud cover, and Beaufort sea state were significant ($P<0.0001$, $P<0.0006$, and $P<0.0021$, respectively), the yearly trend was not ($P = 0.8535$). None of the interaction effects were significant. The parameter estimates for the models with and without year are displayed in Table 4.

Table 3

Results of the weighted analysis of covariance.

Source	df	Sum of squares	Mean square	F value	Prob. >F
Model	5	15397	3079	10.46	0.0001
Area	1	9494	9494	32.24	0.0001
Cloud cover	1	3927	3927	13.34	0.0006
Beaufort	2	4095	2047	6.95	0.0021
Year	1	10	10	0.03	0.8535
Error	54	15900	294		

Table 4

Parameter estimates from (A) the ANCOVA testing year, and (B) the 'best' model (ANOVA) chosen for the simulations. Standard errors are given in parentheses.

Parameter		(A)		(B)	
μ	Mean	−2.1496	(0.3288)	−2.1454	(0.3251)
α_{B1}	Beaufort 0&1	0.0000	—	0.0000	—
α_{B2}	Beaufort 2	−0.0838	(0.3304)	−0.0883	(0.3266)
α_{B3}	Beaufort 3	−1.1344	(0.3516)	−1.1257	(0.3453)
α_{A1}	Area 1 (South)	−1.5338	(0.2701)	−1.5360	(0.2674)
α_{A2}	Area 2 (North)	0.0000	—	0.0000	—
α_{C1}	Clear skies	0.0000	—	0.0000	—
α_{C2}	Cloudy skies	−1.0377	(0.2841)	−1.0454	(0.2787)
δ	Year	+0.0182	(0.0982)	—	—

Analysis of power to detect trends

No trend simulations ($\delta = 0$) To determine the reliability of the simulation procedure to model trends in porpoise abundance, 500 simulated data sets with no yearly trend were created for five, six, eight, and ten survey years, using parameter set (B) in Table 4. The simulated data sets were analyzed using the full

Table 5

Actual α-errors and fractions of positive and negative covariate coefficient estimates (δ) for ANCOVA of 500 random data sets for five, six, eight, and ten simulated survey years.

No. of years	% annual change	Actual α-errors for $\alpha = 0.05$	$\alpha = 0.10$	$\alpha = 0.20$	Fractions of $\pm\ \delta$ values
5	none	0.05	0.10	0.20	0.48/0.52
6	none	0.06	0.11	0.21	0.54/0.46
8	none	0.04	0.10	0.20	0.49/0.51
10	none	0.07	0.12	0.23	0.53/0.47

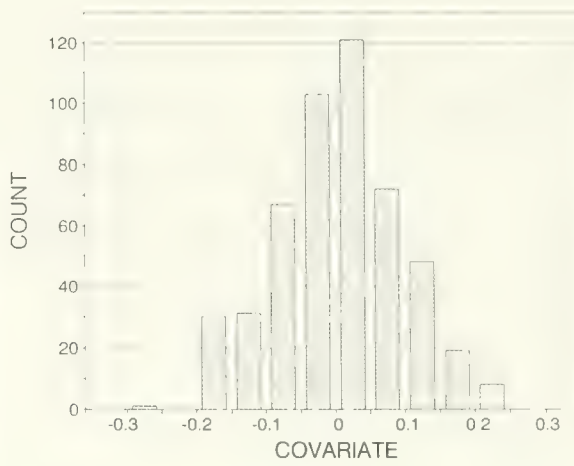

Figure 4

Distribution of covariate estimates (δ) representing yearly change in abundance of harbor porpoise (from ANCOVA) for 500 simulations of five survey years with no annual trend in abundance.

ANCOVA model with a null hypothesis of no trend in abundance. The α-error (Type I error) is the fraction of simulations which falsely detected a trend.

For all four simulations, the resulting α-errors were close to the theoretical ones (Table 5). The average root mean-square-error term obtained for these data sets (16.63) was also close to the error for the actual data (17.01). The estimates of the covariate for year (δ) in the simulated data were approximately normally distributed with a zero mean, as expected (Fig. 4). This confirms that the simulation procedures do not introduce substantial bias into the data or error structure.

Simulations with trends ($\delta \neq 0$) To analyze the power of this procedure to detect given trends, random data sets spanning five, six, eight, and ten years were created with artificial changes in abundance of $\pm 5\%$ and $\pm 10\%$ per year. All other parameters were taken from Table 4, set (B), as above. For each combination of survey years and trend, 500 data sets were created and analyzed with the ANCOVA procedure.

In each simulation, a fraction of the analyses did not detect a trend: this represents the β-error (Type II error). A much smaller fraction detected a trend in the opposite direction of the true trend. The latter presents a special case (dilemma), and we have termed this type of error γ-error (Type III, cf. Carmer 1976). Figure 5 graphically illustrates α, β, and γ for a situation where an increasing trend is occurring and being tested against the null hypothesis in a two-tailed test (in a one-tailed test, γ is zero). The three types of errors are interdependent: as α increases (i.e., the bars in Figure 5 move closer to zero), β decreases, and γ increases.

Power has been defined as the probability of correctly rejecting the null hypothesis when it is false, which numerically is $1 - \beta$ (Rotenberry and Wiens 1985, Peterman 1990ab). However, this definition does not address the error associated with accepting a false alternate hypothesis (γ). In the case of trend analysis, this is the probability of rejecting the null hypothesis (no trend) in favor of a trend in the wrong direction. We therefore suggest that power be defined more precisely to include only the probability of detecting the correct alternate hypothesis, which numerically is $1 - (\beta + \gamma)$.

Using this definition, the power to correctly detect trends in harbor porpoise abundance is displayed in Table 6 for six different levels of α. The values listed under $\alpha = 1.0$ correspond to the fraction of the time that the sign of the covariate is correct, regardless of significance level. At this α-level, the β-error is zero, because the null hypothesis of no trend is always rejected in favor of either an increasing or a decreasing trend. Both power and γ-errors are maximized when $\alpha = 1.0$ (see Discussion below).

At $\alpha = 0.05$, the ability to detect trends in abundance of harbor porpoise is poor (0.07–0.79) for all tested trends and numbers of survey years. This is below the level of power = 0.80 which has been suggested as a minimum standard (Skalski and McKenzie 1982, Peterman and Bradford 1987). Raising α-levels improves the ability to detect trends, but also increases the chance of detecting a trend in the opposite direction of the true trend (γ-error). When $\alpha = 0.05$, γ-errors are less than 0.01 for the levels of change tested. In contrast, at $\alpha = 0.20$, γ-errors range from 0 to 0.05, and with $\alpha = 1.0$, γ-errors are between 0 and 0.33. Both β and γ-errors are reduced with larger trends and more survey years.

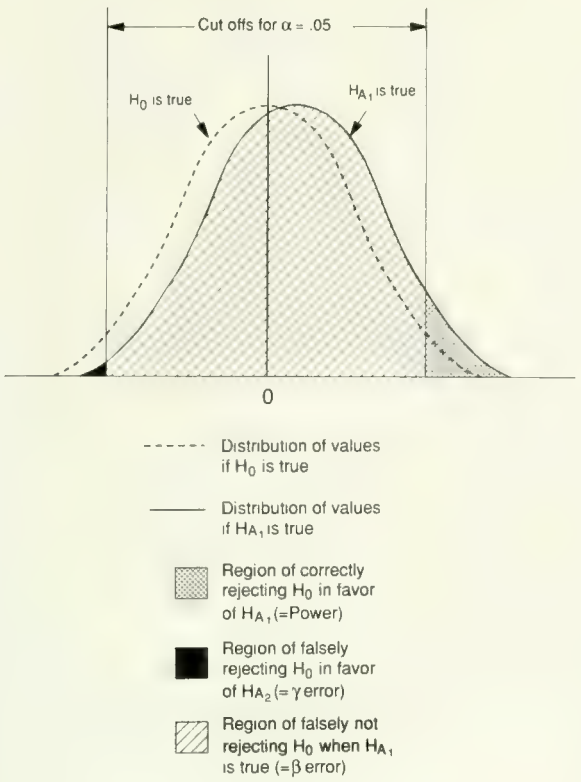

Figure 5

Graphic illustration of the errors associated with a two-tailed test, such as trend analysis. Solid line represents the distribution of coefficients for a hypothetical increasing trend. Dashed line represents the null distribution of coefficients (when there is no trend). Shaded areas represent the three error types, α, β, and γ (see text). H_{A1} represents an increasing trend, H_{A2} represents a decreasing trend, and H_0 represents no trend.

Table 6

Estimated power of the analysis to detect a given trend in harbor porpoise abundance correctly, based on 500 random data sets for each combination of change and number of survey years. Power is defined as $1-(\beta+\gamma)$.

No. of years	% annual change	Power associated with given α-error α = 0.05	0.10	0.20	0.30	0.40	1.0
5	−10	0.17	0.24	0.36	0.43	0.52	0.82
6	−10	0.23	0.35	0.52	0.60	0.68	0.90
8	−10	0.52	0.63	0.74	0.82	0.86	0.98
10	−10	0.79	0.87	0.92	0.95	0.97	1.00
5	+10	0.11	0.18	0.29	0.39	0.47	0.78
6	+10	0.21	0.32	0.45	0.54	0.63	0.89
8	+10	0.46	0.56	0.70	0.80	0.85	0.97
10	+10	0.74	0.82	0.88	0.93	0.96	1.00
5	−5	0.08	0.14	0.22	0.28	0.35	0.70
6	−5	0.10	0.16	0.29	0.38	0.44	0.72
8	−5	0.17	0.27	0.42	0.50	0.59	0.84
10	−5	0.27	0.37	0.55	0.65	0.71	0.91
5	+5	0.07	0.13	0.20	0.27	0.34	0.67
6	+5	0.10	0.16	0.25	0.34	0.40	0.73
8	+5	0.15	0.23	0.35	0.45	0.53	0.83
10	+5	0.25	0.34	0.48	0.57	0.66	0.89

Discussion

The number of years necessary to detect trends in harbor porpoise abundance with the techniques described above will depend on two things: the rate of change to be detected, and the degree of certainty desired. A 5% annual change will be more difficult to detect than a 10% change over the same time period. If a large change must occur before the trend is detected, such methods may be of limited use in the management of populations, and more powerful techniques may be required.

If one does not need the ability to determine both increases and decreases, but merely wishes to determine whether a population is declining (objective 3, Peterman and Bradford 1987), one-tailed statistical tests can be used and will increase statistical power. Alternatively, if one is willing to accept a larger probability of inferring a trend when none is actually present, the power to detect trends can be improved by raising the level of α used to determine statistical significance.

It has been suggested that appropriate levels for α and β should be determined based on the relative costs of committing each type of error (Toft and Shea 1983, Rotenberry and Wiens 1985, Hayes 1987, Peterman 1990b). If the cost of failing to detect a change in abundance is high relative to the cost of falsely detecting a trend for a stable population, then the traditional α-level of 0.05 may be inappropriate. In such cases it may be preferable to minimize β-errors by increasing α. For example, in the context of ecological monitoring, Hinds (1984) suggests that α should be made equal to β. However, it is important to remember that increasing α when power is low also raises γ from virtually zero to potentially large levels. Rather than equalizing α and β, a tradeoff must be made between all three types of error. The magnitude of these errors can be estimated using simulations.

When α is raised to 0.10, ten years of data are sufficient to yield power greater than 0.80 and a γ-error of virtually zero when a 10% annual change is occurring. However, this corresponds to a very large total change in abundance (236% increase or 61% decrease). A

smaller, but still substantial, change of 5% per year (total 155% increase or 37% decrease) would have a very low chance of being detected at this level of α. If small changes are to be detected, then α may have to be set higher.

The most extreme form of raising α-levels is accomplished by considering only the sign of the estimate for the covariate coefficient in the ANCOVA, thus setting $\alpha = 1$. In this case, the direction, rather than the presence, of a trend is tested for. This approach maximizes power, and may be an alternative for situations where power cannot be improved through other means (i.e., increasing the number of surveys conducted). For harbor porpoise trend estimation, the roughly equal fractions of positive and negative covariate coefficient estimates, δ (Table 5) indicate that such an analysis is not biased towards detecting either trend direction.

With $\alpha = 1.0$, power to detect the correct trend in harbor porpoise abundance ranges from 0.67 to 1.00 for 5–10 survey years and ±5% and ±10% annual population changes. Power of 0.80 or higher is achieved with $\alpha = 1.0$ after 5–6 survey years for a 10% annual change, or after 8 survey years for a 5% annual change. However, since the cost of low power in this case is a γ-error, power should be higher than when α is set at the traditional level of 0.05. In this case, eight survey years may provide high enough power to detect an annual 10% change, whereas even 10 years may not yield sufficient power to detect the smaller 5% annual change.

The magnitude of the γ-error when $\alpha = 1.0$ can be demonstrated with Figures 6 and 7. The three curves in these figures represent the distribution of covariate coefficients, δ, for 500 simulated data sets with annual changes of (A) −10%, (B) 0%, and (C) +10%. The γ-error is represented by the area under curves A and C which lies on the incorrect side of zero. If this area is small or equal to zero, as when 10 annual surveys are conducted (Fig. 6), then the analysis will have a high probability of detecting the direction of a trend correctly. However, if the area is large, as when only five annual surveys are conducted (Fig. 7), then the procedure will not be able to detect the direction of trends accurately. The large degree of overlap between the three curves in Figure 7 also reflects the low power to detect trends. The dotted line marks the location of the covariate coefficient estimate (δ) for the 1986–90 survey data. It is apparent that the estimate could reasonably come from any of the three distributions.

Setting $\alpha = 1.0$ is valid only if the costs of interpreting a nonexistent trend in a stable population are small in relation to the costs of failing to detect an existing trend. This may be the case if one needs to determine whether an existing level of take from a commercially exploited population is sustainable. The cost of not detecting a decreasing trend could be extinction of the population and the permanent loss of a resource. On the other hand, eliminating or reducing exploitation on a stable population which is incorrectly thought to be decreasing would cause smaller, short-term costs. In the case of marine mammals in the United States, existing laws mandate that all species be maintained at sustainable levels, so extinction represents an unacceptably high cost.

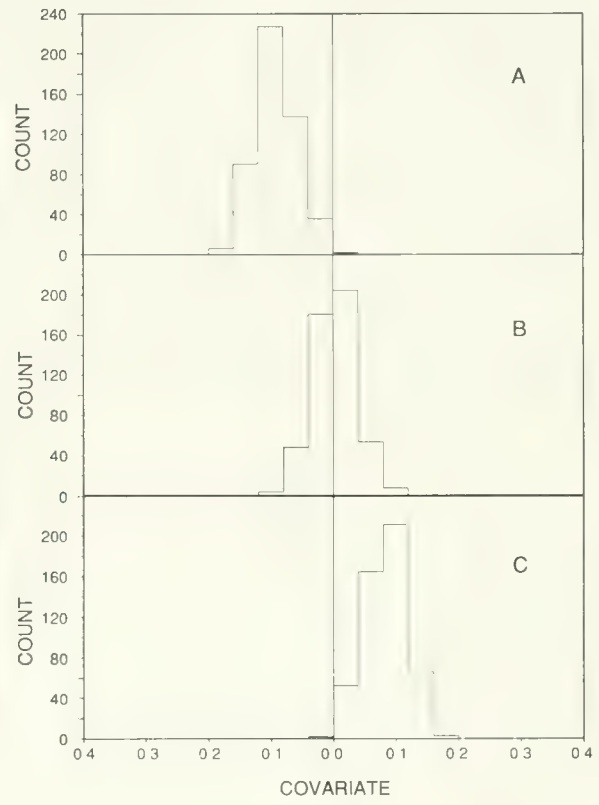

Figure 6

Distribution of covariate estimates (δ) representing yearly change in abundance (from ANCOVA) for 500 simulations each of (A) 10% annual decrease, (B) no change, and (C) 10% annual increase in abundance over 10 survey years. Shaded area under curves A and C which lies on the incorrect side of zero represents the γ-error when $\alpha = 1.0$; here, it is essentially zero.

Several assumptions of the above procedures must be discussed. The most critical assumption is that the five years of data collected during 1986–90 characterize the level of variability expected in a longer time series. In addition, the results of the simulations are only accurate if the ANCOVA model is appropriate. The results indicate that the chosen model fits the data well ($P<0.0001$).

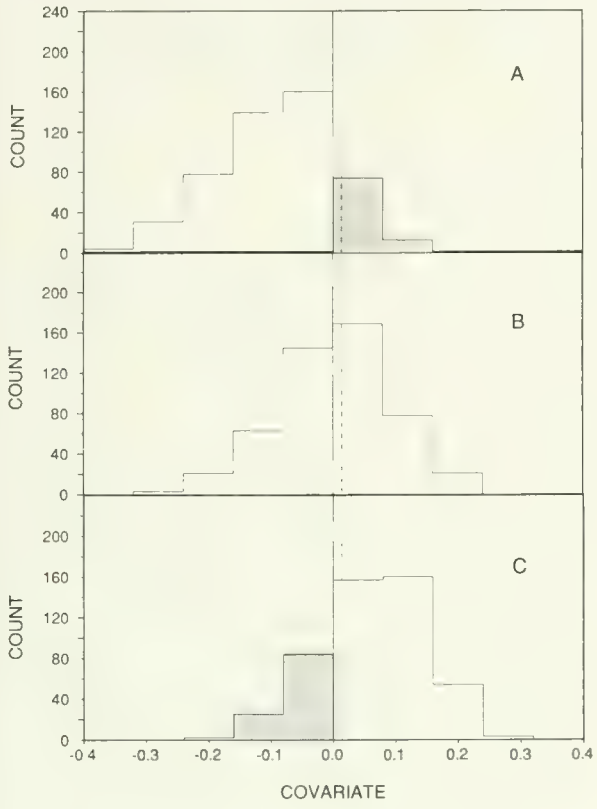

Figure 7

Distribution of covariate estimates (δ) representing yearly change in abundance (from ANCOVA) for 500 simulations each of (A) 10% annual decrease, (B) no change, and (C) 10% annual increase in abundance over five survey years. Shaded area under curves A and C which lies on the incorrect side of zero represents the γ-error when $\alpha = 1.0$. Dashed line marks location along the x-axis of the covariate estimate for actual 1986–90 harbor porpoise data.

The choice of adding the constant 0.001 in the log-transform may at first seem a bit odd, but in fact would be the same as the more familiar transformation $\ln(x + 1)$ if relative abundance had been defined as porpoise per thousand kilometers, rather than porpoise per kilometer. Several other constants were tested to determine if the choice of transformation might influence the analysis. The stepwise procedure yielded the same model in each case. The value 0.001 was chosen because it yielded the most normal distribution of porpoise per kilometer values (Fig. 3B).

This approach to trend analysis also assumes that the fraction of animals visible from the air does not change over time. The probability of detection can be influenced by many factors, particularly sighting conditions, porpoise behavior and group sizes, and observer differences. In our analysis, we controlled for sighting conditions by eliminating poor conditions and stratifying by the remaining ones. Changes in observers between years prevented tests of observer differences. However, based on previous tests with three years of data, they are not believed to be significant (Forney et al. 1989).

Harbor porpoise behavior, including frequencies of active versus inactive behaviors and mean group sizes, has been shown to vary by area and season (Calambokidis et al. 1990, Taylor and Dawson 1984, Sekiguchi 1987). To control for these potential differences, the surveys followed the same transect lines during the same season (autumn) each year. Nevertheless, group sizes in 1989 were significantly different than those in 1987 and 1988 (Kolmogorov-Smirnov test of cumulative distributions, $P = 0.02$ for both tests). The difference appears to be due to a larger percentage of groups containing three or more animals.

If group size affects harbor porpoise sightability, a substantial change in group size distribution could bias the trend analysis, either obscuring a present trend or creating a false one. To test for this possibility, the ANCOVA was repeated excluding the data for 1989. The overall results were similar, with the same final model, similar parameters, and no significant yearly trend ($P = 0.98$). We conclude that this slight difference in group sizes is not likely to have affected our analysis.

Conclusion

The use of simulations allows researchers to estimate appropriate error levels for the analysis of surveys of animal populations. The ANCOVA model we used suggests that no trend in harbor porpoise abundance occurred between 1986 and 1990. However, our simulations show that the power of this model to detect trends using conventional α-levels of 0.05 or 0.10 is poor. Therefore, it is more correct to say that we could not reject the null hypothesis of no trend due to insufficient power.

Power can be increased by raising the acceptable level of α. If only the sign of the coefficient for the covariate year is used to determine the direction of a trend, regardless of significance level, then the ANCOVA has a high probability of detecting trends correctly, particularly with eight or more annual surveys. However, at higher α levels, the probability of detecting a change in the wrong direction (γ-error) increases.

When making decisions, there are distinct trade-offs between the error types which must be evaluated. In trend analysis, power should be defined as $1 - (\beta + \gamma)$ to include only detection of a trend in the correct direc-

tion. If the cost of making an α-error, i.e., falsely concluding that a stable population is increasing or decreasing, is low, α can be increased to increase power. However, attention must be paid to both β and γ-errors as power increases. If γ is relatively large, then power should be greater than the previously suggested value of 0.80.

Additional surveys improve the power to detect trends and reduce γ-errors. Furthermore, if future research can identify and record additional factors affecting observed abundances, such as productivity of the area surveyed (Smith et al. 1986) or ocean temperature patterns (Reilly 1990), this may reduce the variability in the model and increase power.

Future research is planned to continue surveys and search for alternative methods of analyzing these data. The traditional approach to making statistical inference regarding trends has been hypothesis testing with a null hypothesis of no change. As seen in this paper, this is a complicated approach. One must first decide what levels of α, β, and (now) γ one is willing to tolerate. The range of these errors is dependent on many factors, including the level of change to be detected, and the number of years surveyed. Once inference is made, it cannot be presented to others without reference to this bewildering array of decision criteria.

Bayesian statistics (Iversen 1984, Press 1989) may offer an alternative approach to statistical inference, circumventing many of the complications discussed above. Bayesian methods would allow the calculation of the probability distribution of possible trends given the observed data. From this distribution it would be possible to directly calculate the probability that the population is increasing or decreasing. Such methods may be of more value than statistical test results which are highly dependent on the chosen error levels.

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Catch-per-effort and Stock Status in the U.S. North Pacific Albacore Fishery: Reappraisal of Both

Pierre Kleiber
Christina Perrin

La Jolla Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271, La Jolla, California 92038

Abstract.—On reexamining a routine procedure for reporting catch-per-effort (CPE) in the North Pacific albacore fishery, we found evidence that CPE as an index of population size has been subject to a changing degree of bias. The increasing, positive bias in the routinely reported CPE has produced an optimistic, upward trend in this population index during the past decade. A time series of CPE, calculated in a different way, trends downwards. We show that both time series are subject to increasing, positive bias under conditions of an increasing ability of fishermen to locate concentrated patches of albacore. We present evidence that this ability has grown over the past decade, possibly as a result of increasing availability of satellite-based fishing advisories. The divergence of the two time series is explained by a model that shows a different rate of increase in bias in the two cases. The fact that the bias is increasing in the new time series implies that the true population has undergone a more severe decline than is shown by that series.

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Fishery Bulletin, U.S. 89:379–386 (1991).

The Southwest Fisheries Science Center (SWFSC) has been collecting fishery statistics from the U.S. North Pacific albacore fleet for a number of years. Overall catch-per-effort (CPE) and other summary statistics are included in the deliberations of the International North Pacific Albacore Workshops (Bartoo and Watanabe 1989) and are used to indicate the status of albacore stocks in the region. The history of these assessments has been consistently a favorable outlook of increasing abundance for the stocks, although in recent years the workshop has underscored the lack of detailed information about albacore catch in the growing gillnet fishery in the North Pacific.

The U.S. North Pacific albacore fleet consists primarily of jig vessels which vary in length from 25 to over 100 feet. The effect of vessel length on albacore fishing power was investigated by Laurs et al. (1976). They reported significant variability between 10-foot length-classes of jig vessels. Based on relative fishing power estimates for each year, adjusted effort and CPE values were calculated back to 1961. Since that time the calculation of fishing power and concomitant standardization of effort and CPE has become a routine part of reporting the albacore catch and effort statistics by the SWFSC.

In preparation for the 1989 North Pacific Albacore Workshop, we revisited the theory and rationale behind the effort standardization and calculation of CPE to see if the routine procedures continued to be appropriate. We found that even with standardization for fishing power, there was a high degree of residual variability in CPE within the fishing grounds which was not being addressed. Recalculation of the time series of CPE with a rough correction for such variability showed that the optimistic upward trend over the past decade in the original series was replaced by a downward trend. In an effort to reveal which of the two time series is more representative of the true course of the albacore population, we explored the data in more detail to find what might cause the divergence in the two CPE series. This paper is a report of our appraisal of the routine procedure and our reappraisal of the status of the albacore stocks.

Description of the fishery

The U.S. North Pacific albacore fishery is composed of several surface fishing gears. Trolling vessels (jig boats) are by far the most prevalent, followed by baitboats. They operate primarily in the eastern North Pacific. Other North Pacific fleets that harvest albacore include a Japanese

baitboat fleet, operating in the western North Pacific, and wider-ranging Asian longline and gillnet fleets.

Except for the gillnet fleet, catch and effort in the surface fisheries has declined in the past 15 to 20 years. The U.S. commercial catch of albacore dropped from approximately 20,000 metric tons per year in the early 1970s to less than 5000 metric tons in the late 1980s, while effort dropped over the same period from 40,000 boat days to less than 5000 boat days.

The albacore are very patchily distributed, but evolving satellite technology has helped U.S. fishermen to locate areas of high concentration. Albacore tend to migrate along oceanic thermal fronts, and to form transient aggregations in areas where the frontal structures favor local enrichment (Laurs 1983, Laurs and Lynn 1977). These conditions are detectable by satellite (Laurs et al. 1984, Svejkovsky 1988). Over the past decade, increasingly sophisticated fishing advisories have been provided to fishermen. The advisories indicate, from satellite data, the locations of oceanographic conditions conducive to albacore aggregation, and fishermen have been taking increasing advantage of these advisories (Laurs 1989).

The ranges of the population and of the fishing grounds are variable both within the fishing season and from year to year. Albacore in the size range vulnerable to the U.S. fishery are entrained in an annual east-west migration pattern. The U.S. fishery peaks during the summer and autumn months when the albacore are closest to the North American coast. Albacore appear to be separated into northern and southern subgroups divided approximately by the 40°N latitude line (Laurs and Lynn 1977). The timing and extent of albacore migration are variable and without synchrony between the two subgroups. The location of oceanic fronts is also variable. As a result, the boundaries of the fishing grounds are extremely ill-defined and fluid, as is the extent to which the fishing ground overlaps the range of the albacore population. The traditional U.S. fishery is primarily nearshore. However, in the past 10 years, jig boats have been venturing farther offshore, some as far west as the dateline, earlier in the season in an attempt to meet the migrating albacore on their way toward the North American coast.

Theory and methods

The routine procedure for estimating fishing power in the U.S. albacore fleet makes use of a computer program, FPOW, coded by the California Department of Fish and Game and described by Fox (1971) and Berude and Abramson (1972). The basic theory behind this program is described by Robson (1966). The heart of the method is an analysis of variance which seeks to account for variation in the logarithm of CPE due to vessel length-classes, as well as to other factors such as time-area strata. Unlike usual analysis of variance, FPOW concentrates on reporting estimates of the coefficients in the statistical model. These coefficients are the logs of the fishing power of vessel classes relative to that of a reference class (45-foot vessels in this case). FPOW does not list a table of residual variances and F statistics, which would indicate the degree of statistical significance of the various factors. Accordingly, for the most recent year for which we had data (1988), we used a different analysis of variance program (BMDP) to better reveal the significance of variation due to vessel length in relation to other sources of variation.

As we looked into the routine procedure for aggregating catch and effort over all the time-area strata in a year, we found that effort (standardized for vessel length) and catch in the individual strata have been summed over strata, and a pooled CPE given by

$$\mathrm{CPE}_{\mathrm{pooled}} = \frac{\sum c_i}{\sum e_i} \qquad (1)$$

has been calculated, where c_i and e_i are the catch and effort in the i-th stratum. In the case where population density varies between strata, it is well known that such a pooled CPE is not a good population index because even though CPE might be proportional to population density in individual strata, that proportionality is destroyed with a pooled CPE. However, that proportionality can be maintained with a stratified CPE given by

$$\mathrm{CPE}_{\mathrm{strat}} = \frac{1}{N} \sum \left[\frac{c_i}{e_i} \right] \qquad (2)$$

where N is the number of strata (Beverton and Holt 1957:148–151). This is simply the average of CPE-s in individual strata. An effort aggregation scheme that in effect does the same thing has been used for the Japanese longline fishery for albacore (Honma 1974).

Strictly speaking, Equation 2 presumes that there is at least some effort in all strata. When that is not true, estimates should be provided of what CPE would have been in each of the missing strata had the fishery visited them. In the case of the U.S. North Pacific albacore fishery, the fluid nature of the fishing grounds described above makes it difficult to say whether a given stratum should be considered missing or not present in the fishing ground for a particular year. For the purpose of our new CPE series, we ignored the problem by ignoring unvisited strata. However, if the

visited strata were not a random sample of available strata, the average CPE would be biased. To the extent that fishermen are able to locate strata with higher than normal population density, we expect them to favor those strata. Therefore, we expect that our new CPE values are only partially corrected for the effects of heterogeneous population density.

Either of the CPE series would still be useful, even though biased, as long as the bias does not change over time. But as noted above, the character of the fishery has been changing. The declining effort over the past approximately 20 years could lead to differential dropout of the less able fishermen, and the increasing availability and use of advisories in the past approximately 10 years could be increasing the ability of the remaining fishermen. The salient ability in this case is that of locating concentrations of albacore. If that ability has been changing, the bias in both old and new CPE time series must also be changing. We will show that the rate of change in bias is different in the two time series.

It would be useful to document the fact that the fishery is increasingly favoring high-abundance strata. Gulland (1956) suggested that the ratio of pooled to stratified CPE could be used as an index of effort concentration. But in this case we do not have a proper stratified CPE because of the problem of missing strata. We have devised a different favoritism index which is the proportion of the effort in any year that is expended in strata with a CPE above some threshold value, CPE*. The favoritism index in year y is given by

$$\text{favoritism index}_y = \frac{\sum_{i \in T_y} e_i}{\sum_{i=1}^{N_y} e_i};$$

$$T_y = \{i \mid (c_i/e_i) \geq CPE_y^*\} \qquad (3)$$

where T_y is the set of stratum indices for which CPE is greater than CPE_y^*, and CPE_y^* is determined by ranking the strata in year y according to CPE and choosing the minimum CPE of the top 20th percentile of the strata.

Data

Our data source is voluntarily contributed logbook information from the U.S albacore fishery. It is maintained on a database by the SWFSC and covers the years 1961 to 1989. The portion of landings sampled each year varies from 15% to 61%.

For analysis of variance, we used the 1988 data, the most recent year available at the time the analyses were conducted. As with the routine standardization procedure, we selected only jig boat records and organized the data by four large strata—early north, late north, early south, and late south—where the division between the early season and the late season is 1 September, and the division between north and south is 38°N latitude. Again following the routine procedure, within the large strata we treated the data by smaller time-area strata consisting of 3° latitude-longitude squares and half-month time periods, and classified vessels by 10-foot length classes. In contrast to the routine procedure, we maintained records of individual vessels within strata and length classes to allow analysis of variance with replicates. For calculating the CPE time series, we utilized 1° latitude-longitude strata, which is the finest resolution available.

Results and discussion

We conducted several analyses of variance with various subsets of the data, using CPE or ln(CPE) as the dependent variable.* Vessel length appears to be a significant factor in relatively few of these analyses (Table 1) whereas time-area stratum is almost always highly significant (low probability under H_0). Because the two-way analyses were unbalanced (unequal number of replicates), effects of the two factors could be confounded to some extent, and rigorous interpretation of the results is difficult. The salient features of the analyses are (1) that vessel size is of questionable significance as a factor influencing CPE, and (2) that time-area stratum tends to have a much higher statistical significance than does vessel size. In other words, it appears that vessel size does not matter nearly as much as where the vessel is and when.

Regardless of its statistical significance, the practical significance of vessel size in the context of reporting effort and CPE can be tested by seeing whether substantially different results are obtained with and without vessel size standardization. We recalculated the 1961 to 1989 time series without such standardization and found very little difference in CPE trends (Fig. 1). There appears to be little point in standardizing for fishing power even though vessel size may be statistically significant in some cases.

The emphasis on accounting for the effect of vessel size has obscured a more prominent feature of variability in CPE, which is the effect of location and time.

* In the routine standardization, ln(CPE) is the dependent variable, and instances of zero catch with positive effort are ignored.

Table 1

Probability under H_0 (no effect) for vessel class (size) and time-area (strat) from one-way and two-way analyses of variance on various subsets of 1988 North Pacific albacore catch-and-effort data, and either CPE or ln(CPE + 1) as dependent variable.

	1- or 2-way	Source	Early season log(CPE+1)	Early season CPE	Late season log(CPE+1)	Late season CPE
North	1	size	0.15	0.001	0.46	0.42
	1	strat	<0.001	<0.001	<0.001	0.03
	2	size	0.03	<0.001	0.29	0.29
		strat	<0.001	<0.001	<0.001	0.03
South	1	size	0.009	0.035	0.66	0.48
	1	strat	<0.001	<0.001	0.22	0.84
	2	size	—	—	0.57	0.20
		strat	—	—	0.23	0.63

	1- or 2-way	Source	Whole season log(CPE+1)	Whole season CPE
North and South	1	size	<0.001	<0.001
	1	strat	<0.001	<0.001
	2	size	0.30	<0.001
		strat	<0.001	<0.001

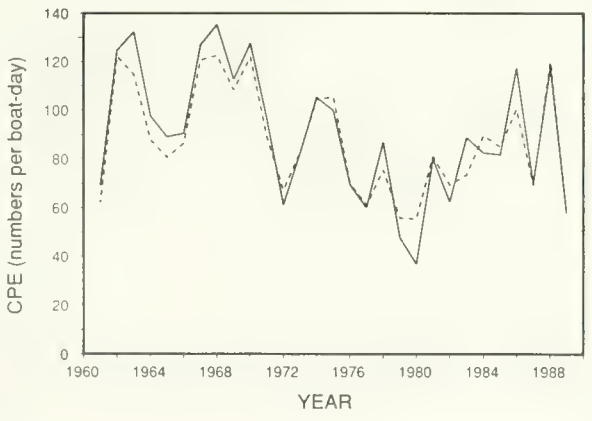

Figure 1

Comparison of original catch-per-effort time series (solid line) with unstandardized catch-per-effort (dashed line) for North Pacific albacore. Both time series are pooled catch-per-effort based on Equation 1. Effort values in the original time series are standardized for size of fishing vessels. Effort values in the other time series are not standardized.

This variability is not taken into account in the existing routine procedure. Our new time series, based on Equation 2 with unvisited strata ignored, gives a noticeably different picture (Fig. 2). The pronounced rising trend since 1978 in the old time series is replaced by a continuing downward trend.

The new CPE time series in Figure 2 was calculated without regard to the time sequence within a fishing season, that is, all spatio-temporal strata in a particular year were entered into the average for that year. If the fishery has not been fully covering the season in which albacore are available in the eastern Pacific, and if there has been a trend in the degree of coverage, then the yearly averages in Figure 2 could reflect that trend rather than a trend in the albacore population. We calculated a detailed time series with a separate CPE_{strat} for each 10-day period (Fig. 3) to look at the temporal pattern of CPE within seasons. In some years such as 1970, 1976, and 1989, it appears that the fishery may have missed a portion of the season of availability of albacore in the eastern Pacific. The CPE was already high at the beginning of the fishery, or the fishery quit before the CPE had tapered off. In most years, however, the fishery appears to have been active from the arrival of the albacore at the fishing ground to their departure. There does not seem to be a trend in the degree of coverage. In any case, it is not clear that variation in the degree of coverage would affect the old and new time series differently.

Another factor that might cause a divergence between the old and new time series of CPE would be an increasing ability of fishermen to locate areas of high albacore abundance. We will demonstrate that this is so with a simple model. Suppose there are two kinds of strata in the fishing ground, ones with low abundance and ones with high abundance, such that the population density within each type is d_l and d_h respectively, and $d_l < d_h$. We assume that CPE is proportional to fish density within the strata. Therefore we can measure d_l and d_h in catch-per-effort equivalents. Suppose further that there are n_l and n_h of each type of stratum in the fishing ground. If the fishery showed no favoritism for either type, then the probability of one unit of effort visiting any particular stratum would be $1/(n_l + n_h)$. We can model favoritism by defining p_l and p_h to be the probabilities that a unit of effort would visit a particular low-abundance or high-abundance stratum. We then let

$$p_l = \frac{1}{n_l + \alpha n_h}; \quad p_h = \frac{\alpha}{n_l + \alpha n_h} \qquad (4)$$

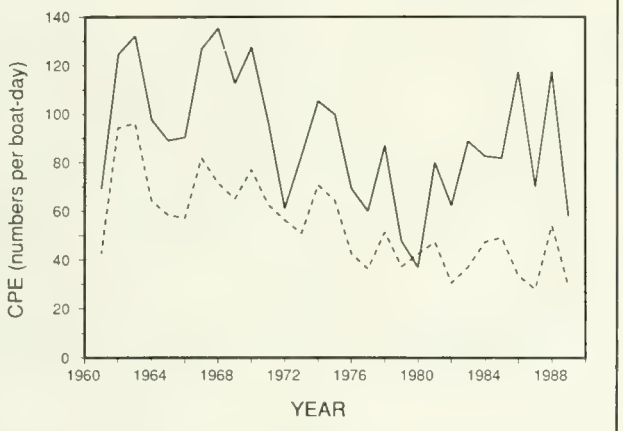

Figure 2

Comparison of original catch-per-effort time series (solid line) with a new catch-per-effort time series (dashed line) for North Pacific albacore. The original time series (CPE_{old}) is the same as the solid line in Figure 1. The new time series (CPE_{new}) is calculated using Equation 2 and ignoring strata with no effort.

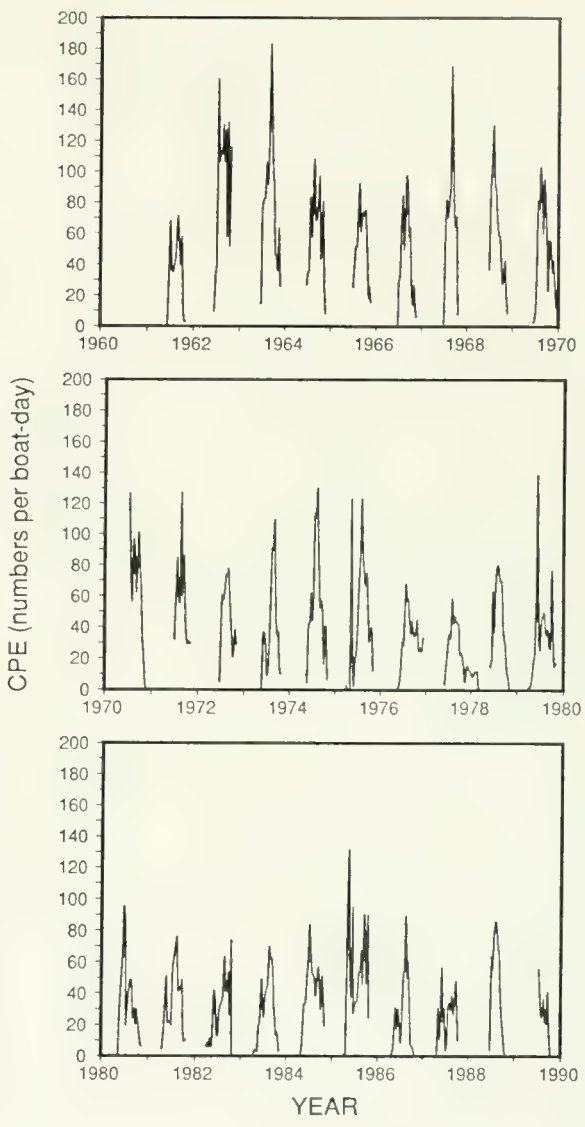

Figure 3

Detailed time series of stratified catch-per-effort for North Pacific albacore calculated for every ten-day period using Equation 2 and ignoring strata with no effort.

where α is a favoritism coefficient. When α equals 1, the probability of a stratum of either type being visited is the same, and there is no favoritism. But as α increases, the chance for any high-abundance stratum is increased at the expense of the chance for any low-abundance stratum. Note that the sum of probabilities over all strata, $n_l p_l + n_h p_h$, is equal to 1, so that it is certain that a given unit of effort will land somewhere in the fishing grounds.

The probability that any particular stratum will receive a particular visit is $n_l p_l$ for low-density strata and $n_h p_h$ for high-density strata. The expected total number of visits is $e_{tot} n_l p_l$ to any of the low-density strata and $e_{tot} n_h p_h$ to any of the high-density strata, where e_{tot} is the total effort expended by the fishery. Therefore,

$$E[C_l] = e_{tot} n_l p_l d_l; \quad E[C_h] = e_{tot} n_h p_h d_h \qquad (5)$$

where C_l and C_h are the catches from all the low-density and high-density strata, respectively, and d_l and d_h are measured in CPE equivalents.

The old CPE is the total catch over total effort. Its expected value is thus,

$$E[CPE_{old}] = \frac{E[C_l] + E[C_h]}{e_{tot}} = n_l p_l d_l + n_h p_h d_h. \qquad (6)$$

To calculate the new CPE, we need the number of strata in each area with at least one visit, v_l and v_h. To get these, we will first derive the number of low- and high-density strata that are missed altogether. The probability that a particular stratum is missed by a particular effort unit is $1 - p_l$ for low-density strata and $1 - p_h$ for high-density strata. The probability that a particular stratum is unvisited by any effort unit, that is, missing in the data, is thus,

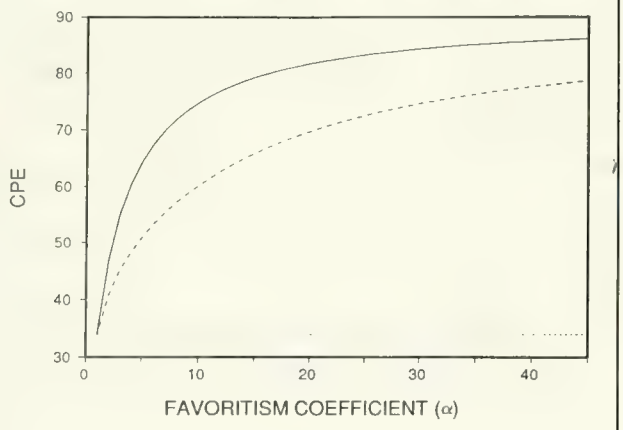

Figure 4

Catch-per-effort for North Pacific albacore predicted by model as function of favoritism coefficient, α, which reflects the ability of fishermen to locate fish concentrations. The expected values of CPE_{new} (solid line) and CPE_{old} (dashed line) are compared with the true mean population density in CPE equivalents (dotted line). The maximum error in the approximation for $E[CPE_{new}]$ is less than 0.7 CPE units in all cases.

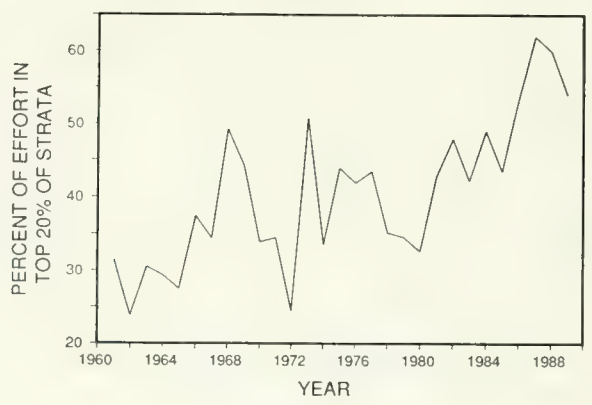

Figure 5

Favoritism index of vessels fishing for North Pacific albacore, calculated using Equation 3. The index measures the degree to which fishermen concentrate on strata with high fish populations. It is the proportion of effort in each year exerted in the top 20th percentile of strata where strata are ranked by catch-per-effort.

$$P[\text{stratum i missing}] = \begin{cases} (1-p_l)^{e_{tot}} & \text{if i in low-density area} \\ (1-p_h)^{e_{tot}} & \text{if i in high-density area.} \end{cases} \quad (7)$$

In each area the expected number of strata with at least one visit is the total minus the expected number of missing strata. Thus,

$$E[v_l] = n_l - n_l(1-p_l)^{e_{tot}}; \qquad E[v_l] = n_h - n_h(1-p_h)^{e_{tot}}. \quad (8)$$

The new CPE is the average over the visited strata of the CPE values observed therein, that is,

$$CPE_{new} = \frac{v_l d_l + v_h d_h}{v_l + v_h}. \quad (9)$$

The functional form of Equation 9 does not allow substitution of expected values of v_l and v_h to get the expected value of CPE_{strat} exactly. However, it has been shown for a similar situation that it is a close approximation as long as the expected number of visited strata is not too small (Deriso and Parma 1988). The expected value of the new CPE is approximated by

$$E[CPE_{new}] \approx \frac{E[v_l]\, d_l + E[v_h]\, d_h}{E[v_l] + E[v_h]} \quad (10)$$

with an error less than $(d_l + d_h)/(E[v_l] + E[v_l])$ based on Deriso and Parma's formulation.

With some straightforward algebra it can be shown that when $\alpha = 1$ (no favoritism), $E[CPE_{old}]$ and $E[CPE_{new}]$ are both equal to the true mean population density (in CPE equivalents), that is,

$$\alpha = 1 \implies E[CPE_{old}] = E[CPE_{new}] = \frac{n_l d_l + n_h d_h}{n_l + n_h}. \quad (11)$$

It can furthermore be shown that as α increases above 1, $E[CPE_{old}]$ and $E[CPE_{new}]$ rise monotonically and approach d_h as α gets large (Fig. 4). Thus, old and new CPE are both unbiased when there is no favoritism; the bias increases at different rates for the two as favoritism increases; and they both approach the same bias as favoritism becomes large.

Relating the model results back to the U.S. North Pacific albacore fishery, we presume that an increasing ability to locate high-abundance strata is equivalent to a rising value of favoritism (α) in the model. The divergence of the old and new time series (Fig. 2) indicates that the effective α has been increasing toward some intermediate level. Changes in the fishery in the past decade—increasing availability and use of fishing advisories and severe decline in effort with the possibility of differential loss of less-able fishermen—are consistent with such a change in α.

In searching for corroborative evidence that the fishery has been increasingly concentrating on high-abundance strata, we found that the favoritism index given by Equation 3 has been tending upwards, particularly over the last decade (Fig. 5). This coincides well with the divergence in the old and new time series of CPE starting around 1979 (Fig. 2). Given this evidence of increasing ability to locate aggregations, the recovery in the old CPE time series in the past decade reflects a change in fishing operations and not a recovery of the albacore stocks. In fact, if the albacore population had just been holding its own over that time, the new time series should also have been rising because it is also subject to increasing positive bias. The fact that it has been declining indicates that the population must have been declining even more rapidly.

Though we have not invented a new population index, free of variable bias, the different effect of bias on our new CPE time series and the original CPE time series has helped reveal a change in fishing operations. This change has markedly affected our interpretation of CPE in the United States North Pacific albacore fishery. To reveal population trends with an unbiased time series requires that we deal with unvisited strata. The difficulties of doing so are great with the type of spatio-temporal variability that we have in the North Pacific albacore fisheries. Attempts are being made (R. Mendelssohn, NMFS Southwest Fish. Sci. Cent., Monterey, CA, pers. commun.) with the inclusion of fishery-independent data (environmental data in this case) to infer CPE in unvisited strata.

Conclusion

We have reexamined the details and justification for a routine procedure for processing catch-and-effort data from the U.S. Pacific albacore fleet. We have found that the use of estimates of fishing power to account for variation in catch rates due to vessel size is of negligible value. Standardizing effort for vessel size has had little effect on the observed time series of effort and CPE in this fishery.

On the other hand, the patchy distribution of albacore is of great importance. In the routine procedure for reporting overall fleet effort, the concentration of effort on areas of high abundance has been dealt with inappropriately, so that CPE trends are unrelated to trends in the population available to the fishery. The new CPE, which is an incomplete correction for concentration of effort, reverses what has been seen as a rising trend in abundance over the past decade.

We have shown that the divergence of the old and new time series is consistent with a fishery for a patchily distributed resource and a growing ability to locate high-density patches. Such a scenario is confirmed by detailed examination of changes in the distribution of catch and effort in the fishery. This change is probably due to increasing use of advisories aimed at locating dense albacore patches, but other possible contributing factors include the differential dropout of less-able fishermen from the fishery or a decreasing representation of less-able fishermen in the sampled landings. Whatever the cause, we have shown that in such a scenario, the original time series would have an increasing positive bias as an index of population, and the new series would also have an increasing positive, but reduced, bias. The nature of the fishery is such that we cannot calculate a reliably unbiased index of population based solely on the fishery data. However, the implication of our results is that the actual trend in the population should have been a more severe decline than is indicated by the new time series.

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Development of Eggs and Larvae of California Halibut *Paralichthys californicus* and Fantail Sole *Xystreurys liolepis* (Pisces: Paralichthyidae)

Debra Oda

Section of Fishes, Natural History Museum of Los Angeles County
900 Exposition Boulevard, Los Angeles, California 90007

Abstract.–Egg and larval development of California halibut *Paralichthys californicus* and fantail sole *Xystreurys liolepis* are described from specimens collected in the nearshore zone of the Southern California Bight (except early-stage eggs, described from reared material). Eggs of both species have spherical unornamented chorions, homogenous yolk, and a single oil globule. Chorion diameters of *P. californicus* and *X. liolepis* eggs are 0.64–0.83 mm and 0.72–0.90 mm, respectively. Respective oil globule diameters are 0.09–0.16 mm and 0.14–0.24 mm. Initial embryonic pigmentation patterns are similar; however, distinctive pigment patches develop in the dorsal and ventral finfolds and at the tail tip on late-stage *X. liolepis* embryos. Larvae of *P. californicus* can be distinguished from those of *X. liolepis* at all stages of development. Internal notochord pigment is easily observed in *P. californicus* but is not visible in *X. liolepis*; sphenotic spines are present in *P. californicus* but absent in *X. liolepis*. Body shape, robust in *X. liolepis* and laterally compressed in *P. californicus*, and external pigmentation, heavier in *X. liolepis*, separates flexion and postflexion specimens.

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Fishery Bulletin, U.S. 89:387–402 (1991).

The California halibut *Paralichthys californicus* (Ayres) is an important sport and commercial fish, ranging from the Quillayute River, Washington (Miller and Lea 1972, Eschmeyer et al. 1983), to Almejas Bay, Baja California (LACM 38108-8). In the southern California portion of the range, the eggs and larvae of *P. californicus* are relatively abundant within the nearshore zone (Gruber et al. 1982, Barnett et al. 1984, Lavenberg et al. 1986). However, similarities between the eggs and larvae of *P. californicus* and the fantail sole *Xystreurys liolepis* Jordan and Gilbert may have caused previous identifications of these two species to be confused (Lavenberg et al. 1986), particularly within the geographical overlap of their ranges (*X. liolepis* ranges from Monterey Bay, California to the Gulf of California; Miller and Lea 1972, Eschmeyer et al. 1983). Early-life-history information has been published for both species, but it has not been adequate to separate them at all stages. Ahlstrom and Moser (1975) illustrated a series of four *P. californicus* larvae, but the two smallest specimens (2.5 and 3.8 mm) do not fit pigmentation characters that I will present for *P. californicus*. Ahlstrom et al. (1984) illustrated a postflexion larva of each species and included information on the eggs (chorion and oil globule size, chorion and yolk texture) of *P. californicus* and the larvae of both species (number of elongate dorsal fin rays and sizes at hatching, flexion, and transformation). Eggs of *P. californicus* were erroneously reported as demersal rather than pelagic in Frey (1971).

My purpose is to provide descriptions of the eggs and larvae of *Paralichthys californicus* and *Xystreurys liolepis* and to give characters to separate them from each other and from other commonly occurring fish eggs and larvae in the coastal waters of southern California.

Materials and methods

The main source of material for this study was provided by the Bightwide Ichthyoplankton Program at the Natural History Museum of Los Angeles County (LACM). Beginning in 1978, ichthyoplankton sampling within the Southern California Bight was carried out in nearshore waters (at depths ranging from 8 to 36 m, extended to 75 m in 1981). Samples were collected in discreet depth and oblique tows using manta, bongo, and auriga frames equipped with nets of 333 μ or 1/8-inch stretch mesh (Brewer and Smith 1982, Love et al. 1984, Lavenberg et al. 1986). Plankton samples were fixed in standard 5% buffered formalin on board ship. Most of the samples were maintained

in 5% buffered formalin, but beginning in August 1983 bongo samples (333μ mesh nets) were transferred to 70% ethanol within two weeks of collection.

Collections also were made off King Harbor, Redondo Beach, California, on 12 March and 9 September 1985, using a 1-m plankton net (with 333μ mesh) towed at the surface. Samples of live plankton were brought to the King Harbor Research Laboratory where the fish eggs were removed and separated into types. Each type was reared separately at ambient sea temperature (~16°C), sampled periodically, and fixed and preserved in 5% buffered formalin.

Additional material was generated from spawning brood stock at the King Harbor laboratory. Adults of *Paralichthys californicus* and *Xystreurys liolepis* were maintained and artificially induced to spawn in April (*P. californicus*) and November (*X. liolepis*) 1985. The resulting eggs and larvae were reared in 4-L containers at 16–18°C. Eggs were sampled every two hours, and the larvae were sampled irregularly. These samples were fixed in 5% buffered formalin and preserved in 70% ethanol or 5% buffered formalin.

Table 1
Egg measurements of *Paralichthys californicus* and *Xystreurys liolepis* (diameters in mm).

	N	Chorion	Yolk mass	Oil globule
Paralichthys californicus				
Preserved in 5% formalin				
Field-collected material	1	0.82	0.67	0.14
Reared material	164	0.68–0.83	0.60–0.70	0.12–0.16
Preserved in 70% ethanol				
Field-collected material	70	0.64–0.80	0.40–0.68	0.09–0.12
Reared material	63	0.72–0.77	0.41–0.51	0.10–0.12
Xystreurys liolepis				
Preserved in 5% formalin				
Field-collected material	4	0.83–0.90	0.64–0.72	0.18–0.24
Reared material	278	0.82–0.90	0.65–0.74	0.18–0.24
Preserved in 70% ethanol				
Field-collected material	22	0.72–0.86	0.42–0.56	0.14–0.17
Reared material	70	0.76–0.80	0.50–0.60	0.14–0.17

Descriptions of both species are based primarily on field-collected material as studies of other taxa have noted differences in the appearance of field and reared material (Butler et al. 1982, Watson 1982, Caddell 1988). Field-collected postflexion larvae were identified with the aid of meristic counts. The developmental series was completed by working back towards smaller specimens following the sequential development of pigmentation, morphology, and morphometric patterns. Characters used to identify the earliest yolksac larvae also were used to identify embryos of late-stage eggs. I was unable to identify early-stage eggs from the field collections, so these eggs are described from reared material.

Measurements were made using a Wild M8 Stereomicroscope equipped with a measuring eyepiece. Three measurements were taken on each egg: chorion, yolk, and oil globule diameter. Measurements were made by manipulating the egg so that the oil globule faced up with the embryo at the bottom of the egg and perpendicular to the measurement grid. Larval measurements were made using definitions and methods employed by Moser and Ahlstrom (1970), Ahlstrom et al. (1976) and Leis and Rennis (1983).

The larval period is divided into three stages (preflexion, flexion, and postflexion) based on caudal fin development (Kendall et al. 1984). Prior to notochord flexion, i.e., preflexion, larval length is measured from snout tip to notochord tip and designated NL (notochord length). During flexion, larval length is measured from snout tip to the tip of the notochord or to the posterior margin of the developing hypurals, whichever is longer, and is designated FL (flexion length). The designation SL (standard length) is used for postflexion larvae and is measured from the snout to the posterior margin of the hypurals (now approximately perpendicular to the longitudinal axis of the body). Measurements given in this paper are followed by one of these designations in order to specify the developmental stage of the specimen. All measurements are expressed in millimeters (mm). Separate measurement tables are provided for eggs and larvae preserved in 5% buffered formalin and 70% ethanol because eggs and larvae preserved in ethanol shrink more than those preserved in formalin (Rounds et al. 1984).

Eggs were staged using the method Ahlstrom (1943) proposed for the pilchard. Larvae were cleared and stained following Potthoff (1984), but specimens were left in the acidic alcian blue solution for only two hours to minimize decalcification.

Results

Egg descriptions

Paralichthys californicus Eggs of *Paralichthys californicus* are pelagic and possess a smooth spherical chorion (0.64–0.83 mm), homogenous yolk (0.40–0.70 mm), and a single oil globule (0.09 - 0.16 mm, Table 1).

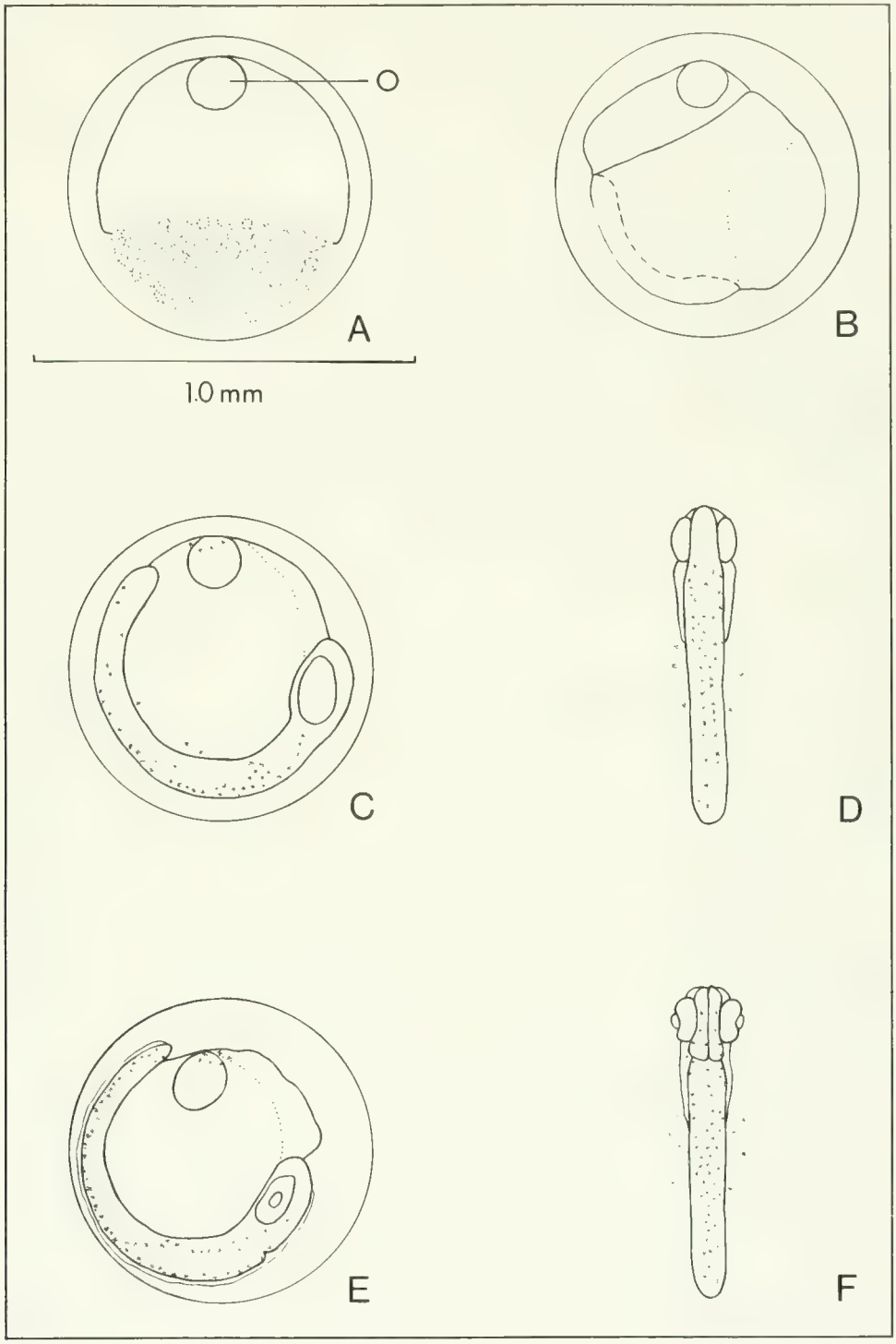

Figure 1
Eggs of *Paralichthys californicus* (o = oil globule): (A) stage II (LACM 44978), (B) stage IV (LACM 44978), (C) stage VI (LACM 44978), (D) dorsal view of embryo, stage VI (LACM 44978), (E) stage VII (LACM 047 88 15 OB 02S), (F) dorsal view of embryo,stage VII (LACM 047 88 15 OB 02S).

The embryonic shield is first visible as a thickening in the blastoderm when the germ ring encloses approximately 70–80% of the yolk (stage IV, Fig. 1B). The eyes and 10–15 somites are visible at about the time the blastopore closes (stage VI). At the end of stage VI, the lateral and posterior margins of the tail are defined, 15–20 somites are present, and pigment develops on the dorsal surface of the embryo posterior to the eyes and on the yolk near the oil globule and off the lateral margins of the body (Figs. 1C,D).

As the tail develops and separates from the yolk (stage VII), a thin finfold becomes visible, the midbrain shows definition, lens primordia form, and 20–25 somites are present. Pigment on the yolk, previously

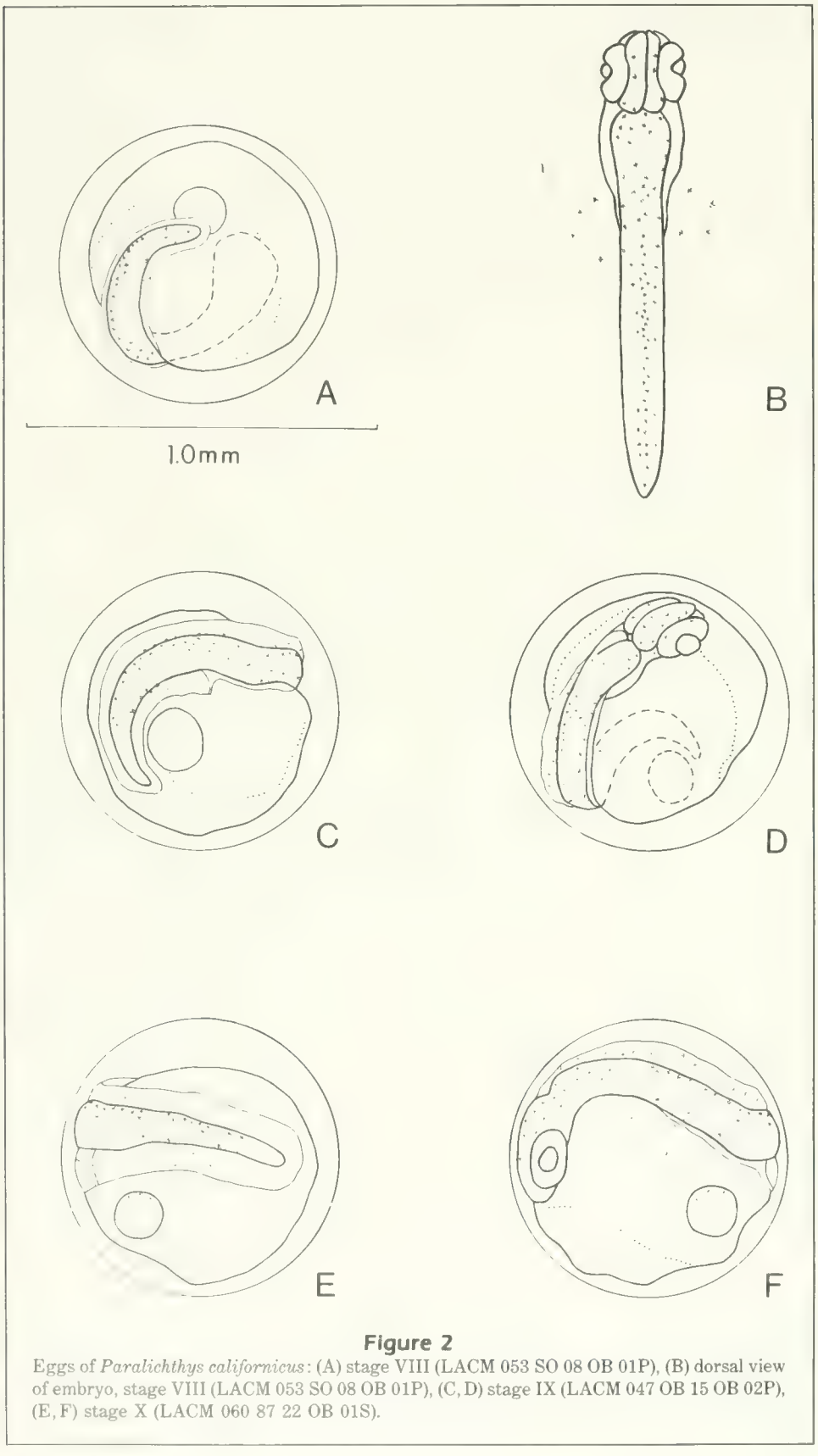

Figure 2
Eggs of *Paralichthys californicus*: (A) stage VIII (LACM 053 SO 08 OB 01P), (B) dorsal view of embryo, stage VIII (LACM 053 SO 08 OB 01P), (C, D) stage IX (LACM 047 OB 15 OB 02P), (E, F) stage X (LACM 060 87 22 OB 01S).

located near the oil globule, encircles and then migrates onto the side of the oil globule nearest the embryo. Pigment on the embryo develops from the eyes to the first somites along the dorsal and dorsolateral surfaces, posteriorly along the dorsum to the tip of the tail, and on the ventral midline of the free portion of the tail (Figs. 1E, F).

When stage IX begins, pigment first migrates into the dorsal finfold between the nape and an area about three-fourths the distance from snout to tail tip and into the ventral finfold opposite the posteriormost dorsal finfold melanophores (Figs. 2C, D). The migration of pigment into the finfolds continues during stage X (Figs. 2E, F), forming a continuous row of melanophores in the dorsal finfold and a patch of pigment in the ventral finfold.

Xystreurys liolepis *Xystreurys liolepis* eggs are pelagic with a smooth chorion (0.72–0.90 mm), homogenous yolk (0.42–0.74 mm), and a single oil globule (0.14–0.24 mm, Table 1). Early- through mid-stage development of *X. liolepis* eggs (stages II–VIII, Figs. 3A–F, 4A, B) is similar to that of *Paralichthys californicus* (Figs. 1A–F, 2A, B) with few differences in the developmental sequence of the embryo, pigment, or oil globule detected. At approximately stage IX, pigment patterns of *X. liolepis* embryos begin to differ diagnostically from those of *P. californicus*.

Melanophore migration into the medial finfolds oc-

curs approximately two-thirds the distance from snout to tail tip in stage IX *Xystreurys liolepis* eggs (Figs. 4C, D). Pigment is present between the eyes, dorsally and dorsolaterally from the eyes to the pectoral region, along the dorsal midline to near the tip of the tail, along the yolk/body interface, on the postanal ventral margin, and at the tail tip (usually on both the dorsal and ventral margins).

At stage X (Figs. 4E, F), melanophores are present in the dorsal finfold at the nape and in both medial finfolds in an area approximately two-thirds of the distance from snout to tail tip. Postanal ventral margin melanophores are generally absent except at the tip of the tail.

Egg comparisons

The larger chorion and oil globule of *Xystreurys liolepis* eggs usually distinguishes them from *Paralichthys californicus* eggs (Table 1), although some overlap exists. Pigmentation patterns of the two species are similar until stage IX, when *X. liolepis* embryos (Fig. 4C) develop heavier pigment at the tail tip and patches of dorsal finfold pigment; pigment is present throughout the dorsal finfold in *P. californicus* (Figs. 2C, D). In addition, stage X *P. californicus* embryos typically have postanal ventral melanophores (Fig. 2E), whereas *X. liolepis* lack pigment along the postanal ventral margin except at the tip of the tail (Fig. 4E).

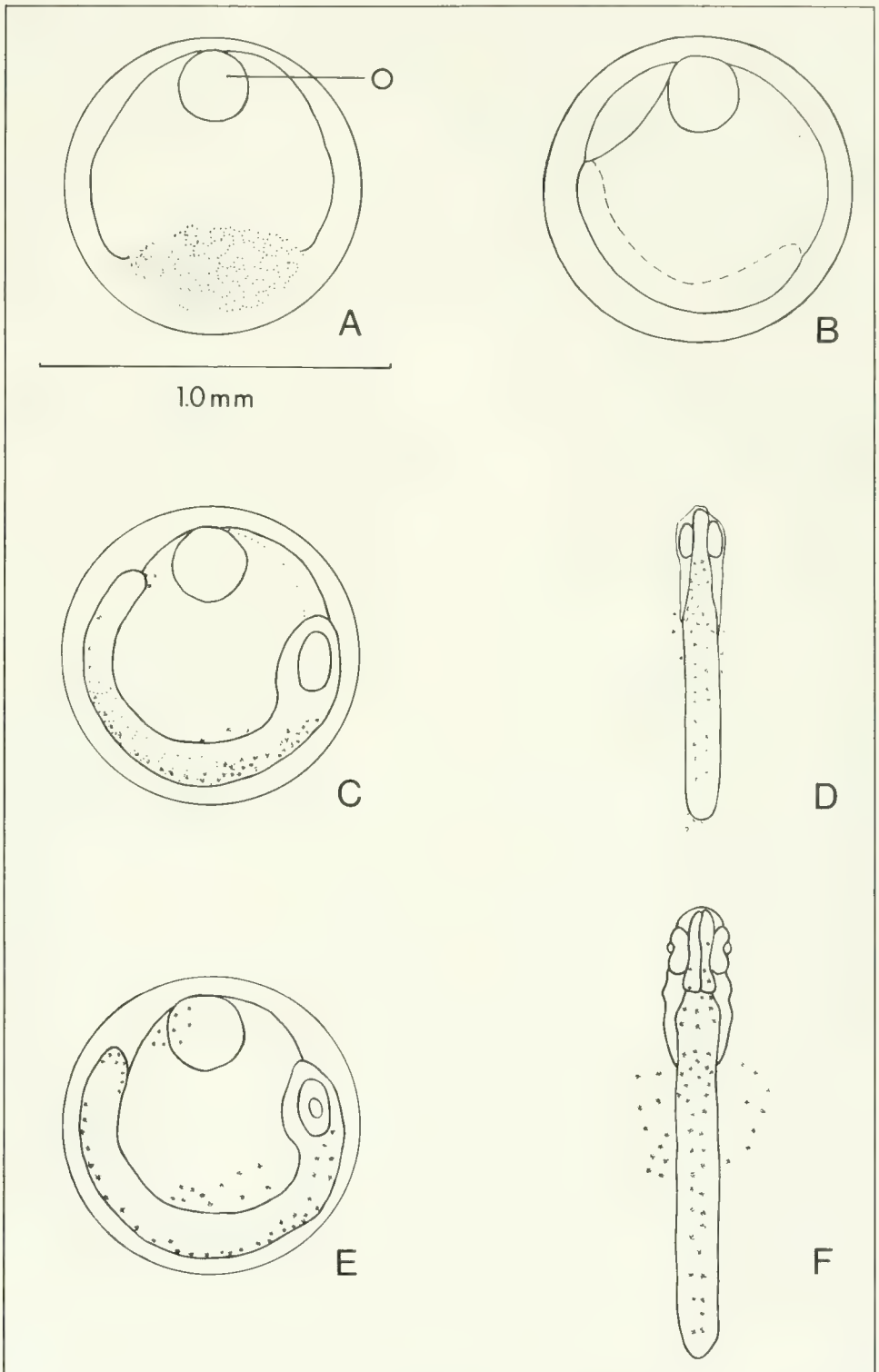

Figure 3
Eggs of *Xystreurys liolepis* (o = oil globule): (A) stage II (LACM 44979), (B) stage IV (LACM 44979), (C) stage VI (LACM 44980), (D) dorsal view of embryo, stage VI (LACM 44980), (E) stage VII (LACM 44980), (F) dorsal view of embryo, stage VII (LACM 44980).

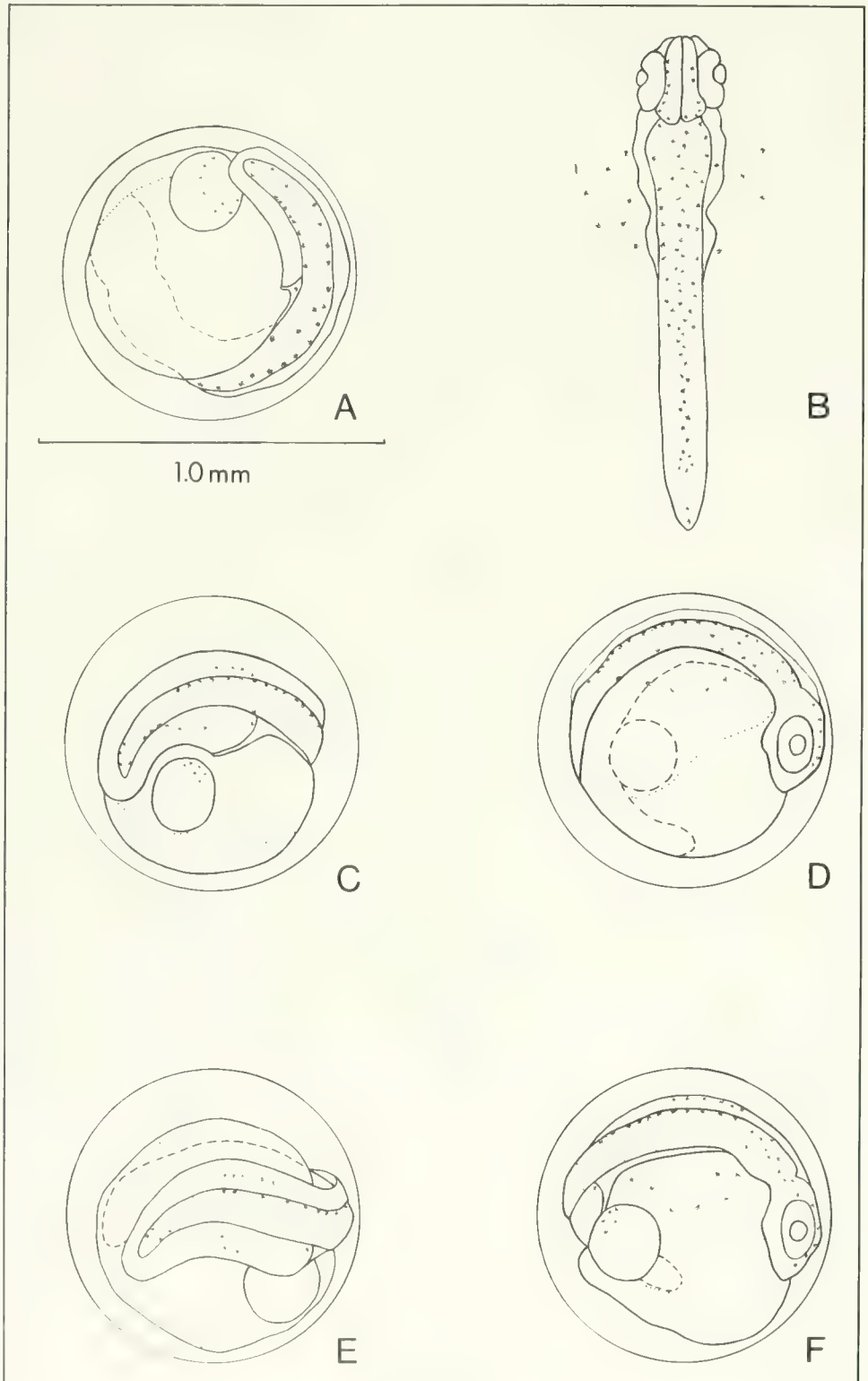

Figure 4
Eggs of *Xystreurys liolepis*: (A) stage VIII (LACM 039 88 22 OB 02S), (B) dorsal view of embryo, stageVIII (LACM 039 88 22 OB 02S), (C, D) stage IX (LACM 050 88 22 OB 01S), (E, F) stage X (LACM 050 88 15 OB 01P).

The eggs of most fishes in the Southern California Bight have not been described; however, the LACM ichthyoplankton group has designated types for the later stages (VII–XI) of eggs commonly collected in the nearshore zone. At these stages, *Paralichthys californicus* and *Xystreurys liolepis* can be separated from the other egg types based on chorion size and texture, yolk homogeneity, oil globule size and position, and pigmentation patterns on the embryo, yolk, and oil globule. Prior to stage VII, identifications are not yet possible.

Descriptions of the two species are based primarily on field-collected material; reared material also was examined. No differences were noted in the sizes of chorion, yolk, or oil globules between the field and reared eggs of either species. Developmental differences of field and reared material for early-stage eggs (less than stage VII) were not determined because of the inability to identify the early-stage eggs from the field material. Pigmentation was similar for field and reared specimens of later stage (VII–X) eggs of both taxa. The field material, however, contained stage X eggs of both species, whereas the reared material hatched at stage IX.

Information is available on the eggs of three other species of *Paralichthys*: *P. dentatus* (Smith and Fahay 1970), *P. olivaceus* (Pertseva-Ostroumova 1961 and Mito 1963) and *P. microps* (Munoz et al. 1988). Eggs

of *P. dentatus* and *P. olivaceus* share similar general morphology and pigmentation with those of *P. californicus*. However, their eggs are slightly larger than *P. californicus* and *P. microps*, and have a larger oil globule than *P. californicus*.

Larval descriptions

Paralichthys californicus

Morphology Preflexion larvae initially are slender (BD ~20% BL) but develop into deep-bodied postflexion larvae (BD 34–39% BL, Table 2). Throughout development larvae are noticeably laterally compressed (HW 12–15% BL). The straight tubular gut of early preflexion larvae develops a coil later in preflexion. The ratio of preanal length to body length remains relatively constant (~45%), but head length increases (from 20 to 30%).

Myomere counts range from 34 to 36. Double-stained specimens (Table 3) have 10 precaudal vertebrae and 24–25 caudal vertebrae.

Table 2

Paralichthys californicus: Morphometric ratio ranges by stage and size (mm). Body length = BL, preanal length = PL, head length = HL, body depth = BD, head width = HW; YS = yolksac, NL = notochord length, FL = flexion length, SL = standard length.

			Range				Mean			
Stage	Preservative	*n*	PL/BL	HL/BL	BD/BL	HW/BL	PL/BL	HL/BL	BD/BL	HW/BL
YS										
2.00–2.99	Formalin	5	42.6–45.8			7.7–10.3	44.3			9.2
	EtOH	11	35.9–45.2			7.6–11.1	40.3			9.2
NL										
2.00–2.99	Formalin	5	41.4–56.7	17.6–25.4	15.9–24.0	10.6–17.4	46.6	20.7	19.4	13.2
	EtOH	9	37.4–47.5	16.5–24.7	17.1–28.8	9.5–16.0	42.4	20.2	20.5	12.6
3.00–3.99	Formalin	10	43.7–53.1	19.6–26.4	17.1–31.0	12.6–19.3	47.8	23.0	22.7	14.7
	EtOH	10	38.0–48.8	19.6–26.4	19.2–31.5	13.3–16.7	42.9	21.7	24.9	14.7
4.00–4.99	Formalin	9	43.4–49.4	21.1–28.4	21.5–32.1	13.6–15.8	45.6	23.3	24.8	14.6
	EtOH	4	41.0–44.8	24.2–25.4	26.3–32.2	14.3–16.0	43.2	24.6	30.5	15.4
FL										
4.00–4.99	Formalin	1	47.9	26.7	32.6	15.1	47.9	26.7	32.6	15.1
	EtOH	4	40.6–46.6	21.2–27.6	27.9–33.2	13.8–14.9	43.6	23.8	31.0	14.3
5.00–5.99	Formalin	7	39.2–51.5	21.2–26.2	26.2–32.1	13.2–15.4	43.0	24.6	29.0	14.0
	EtOH	5	38.3–46.3	23.8–27.9	30.5–34.7	13.0–16.3	42.0	25.5	32.9	13.3
6.00–6.99	Formalin	4	41.9–43.3	21.9–28.0	28.3–38.6	13.0–13.8	42.7	25.5	32.9	13.3
SL										
4.99–6.99	Formalin	4	38.3–47.0	27.4–32.2	34.6–43.3	13.1–15.0	42.9	29.8	38.7	13.9
	EtOH	4	40.2–50.3	27.2–34.1	32.4–45.5	12.5–17.8	43.5	30.5	38.6	15.6
7.00–7.99	Formalin	9	35.4–46.2	25.7–30.0	33.3–40.9	11.0–12.9	41.4	28.8	35.8	11.8
8.00–8.99	Formalin	3	30.8–34.7	27.5–28.7	34.0–34.7	13.4–15.2	33.3	28.6	34.0	13.4

Table 3

Meristics of *Paralichthys californicus* based on double-stained larvae.

		Fins						
Length	Vertebrae	Dorsal	Anal	Caudal	Pelvic	Pectoral	Branchiostegals	Gill raker
3.9 mm NL	–	–	–	–	–	Bud	–	–
4.4 mm NL	–	3	–	–	–	Bud	–	–
4.6 mm NL	–	4	–	–	–	Bud	2	–
6.3 mm FL	10 + 24	11	–	6 + 6	Bud	Bud	7	5
6.5 mm FL	10 + 25	8	23	7 + 8	Bud	Bud	7	7
7.0 mm SL	10 + 25	53	33	9 + 8	3	Bud	7	10
8.1 mm SL	10 + 25	74	57	10 + 8	6	Bud	7	12

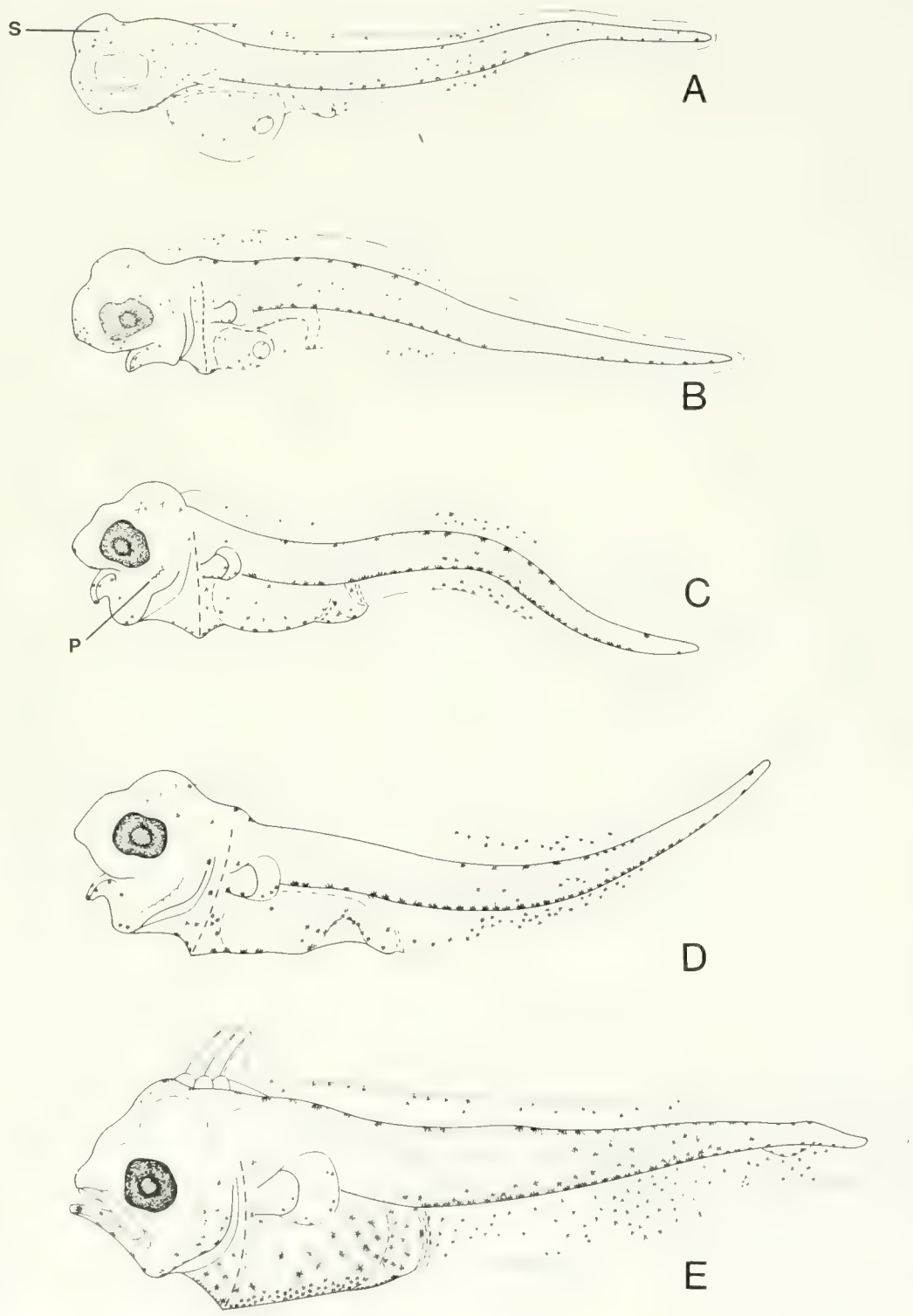

Figure 5

Paralichthys californicus larvae (S = sphenotic spines, P = preopercular spines): (A) 2.0 mm YS (LACM 052 SO 22 OB 02S), (B) 2.0 mm YS (LACM 048 88 75 OB 02S), (C) 2.2 mm NL (LACM 046 87 22 OB 02P), (D) 2.5 mm NL (LACM 048 OB 36 OB 01S), (E) 4.5 mm NL (LACM 048 87 75 OB 01S). (Note: Lightly stippled melanophores represent internal pigment.)

Fin and spine formation Anlagen of the anteriormost dorsal fin rays form at about 3 mm NL. The elongate second through sixth dorsal rays develop first, followed by the first ray and anlagen for the remainder of the dorsal fin and for the anal fin. The remaining rays begin to form at approximately 5–6 mm FL; development is anterior to posterior. The full complement of dorsal fin rays is complete by ~8 mm SL (Table 3).

Larvae develop a series of three sphenotic spines. The dorsal-most spine appears in yolksac larvae just prior to or at the time the lower jaw forms (Fig. 5A). The middle and ventral-most spines develop on first feeding preflexion larvae, and during this stage the spines are relatively easily seen (Figs. 5C, D). The relative size of the spines decreases and they become difficult to locate by about the time the anlagen of the first dorsal fin rays form (Fig. 5E). The spines usually are not visible in late postflexion larvae when eye migration begins (~7–8 mm SL); the developing head melanophores obscure the minute spines (Fig. 6C).

Spines on the posterior margin of the preopercle are visible by ~2.5 mm NL (Fig. 5C). Five to seven spines are present on the lower margin of the bone, and additional spines form on the upper margin at about 5 mm FL (Fig. 6A). Opercular spines, present on postflexion larvae at approximately 6–7 mm SL, usually form along the posterior opercle margin. Another cluster of spines develops at the dorsal margin of the opercle. Opercular spines are not easily visible unless the specimen is stained.

The full complement of 10 + 8 principal caudal rays is present by about 8 mm SL. A splinter ray, attached to the ventralmost ray, is not included in this count.

Pigmentation Larvae are characterized by a row of internal melanophores on the dorsal surface of the notochord. This pigment first appears in late yolksac larvae (Fig. 5B), forms a complete row in the early preflexion stage (Fig. 5C), and remains visible through the body musculature for the entire larval period.

Pigment in the dorsal finfold of yolksac larvae varies from a continuum of melanophores from the nape to mid-tail, to two distinct patches, one at the nape and the other even with the ventral finfold patch, located about mid-tail (Figs. 5A, B). Finfold pigment increases during preflexion and by the end of the stage is present throughout the medial finfolds (Fig. 5E). During flexion, melanophores form on the elongate dorsal fin rays and anal fin anlage (Fig. 6A).

Some melanophores present on the dorsal midline of newly hatched larvae migrate ventrally to form a double row of postanal ventral pigment extending from the vent to a point about mid-tail. Lateral melanophores are located opposite the posteriormost ventral pigment (Fig. 5B). Early in the preflexion stage, the rows of ventral melanophores increase in length, merging with pigment at the tail tip (Fig. 5C). Rows of dorsal and ventrolateral pigment develop and extend from the nape and anus, respectively, to the last myomere (Fig. 5E). Dorsolateral melanophores form during the postflexion stage (Fig. 6C).

Melanophores are present on the yolk and peritoneum of early yolksac larvae and form on the gut and ventral midline, from isthmus to anus, in preflexion larvae (Fig. 5C). Except for the melanophores that form on the lower jaw of yolksac larvae (Fig. 5B), pigment on the head and snout is sparse.

Xystreurys liolepis

Morphology Preflexion larvae are slender (BD ~20% BL), then transform into robust, deep-bodied flexion and postflexion larvae (BD ~45–48% BL, Table 4). Head width varies from about 15% to 20% BL. Gut shape matures from straight tubular to coiled in preflexion larvae; preanal length remains relatively constant, ~45% BL, and head length increases from ~20 to 32% BL.

Myomere counts range from 37 to 39; double-stained specimens (Table 5) have 11 precaudal vertebrae and 26–27 caudal vertebrae.

Fin and spine formation Anlagen for the first dorsal fin rays are formed by ~4 mm NL. The second through the sixth or seventh rays are elongate and develop first, followed by the first dorsal fin ray, and the anlagen for the remainder of the dorsal fin and anal fin. Fin ray formation proceeds posteriorly, and the entire complement of dorsal and anal fin elements are complete by approximately 8 mm SL (Table 5).

Primordia for the developing hypural bones are first visible as a thickening in the ventral finfold, and the incipient caudal rays typically form at 5–5.5 mm FL. The full complement of 10 + 8 principal caudal rays usually is complete around 7 mm SL; a splinter ray on the ventralmost ray is present but not included in this count.

The pectoral bud differentiates into a base and blade between 2 and 2.5 mm NL. The largest larva in the LACM ichthyoplankton collection, 8.9 mm SL, has no pectoral fin rays.

Spines are visible on the posterior margin of the preopercle in preflexion larvae by 2–2.5 mm NL (Fig. 7C). The spines are minute in specimens larger than 7 mm SL.

Pigmentation Three patches of finfold pigment, in the dorsal finfold near the nape, and in both the medial finfolds at about mid-tail, are dense in yolksac larvae (Figs. 7A, B) but less concentrated in preflexion individuals (Fig. 7C). Additional melanophores develop in the dorsal finfold during the preflexion period and

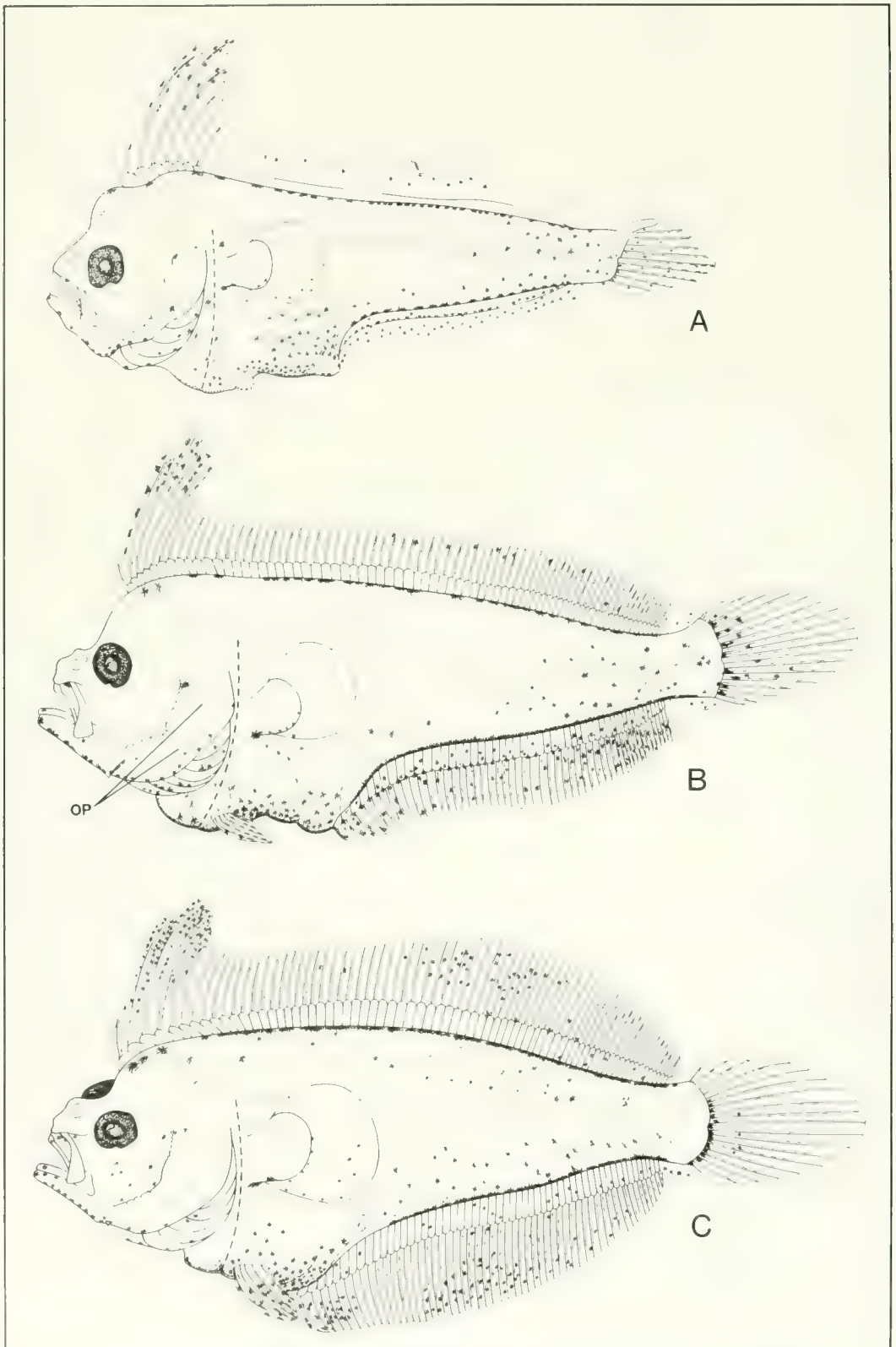

Figure 6

Paralichthys californicus larvae (O = opercular spines): (A) 5.4 mm FL (LACM 048 87 36 OB 02P), (B) 6.6 mm SL (LACM 044 87 22 OB 01P), (C) 8.7 mm SL (LACM 023 RB 15 MA 01). (Note: Lightly stippled melanophores represent internal pigment.)

Table 4

Xystreurys liolepis: Morphometric ratio ranges by stage and size (mm). BL = body length, PL = preanal length, HL = head length, BD = body depth, HW = head width, YS = yolksac, NL = notochord length, FL = flexion length, SL = standard length.

			Range				Mean			
Stages	Preservative	*n*	PL/BL	HL/BL	BD/BL	HW/BL	PL/BL	HL/BL	BD/BL	HW/BL
YS										
1.00–2.99	Formalin	4	37.6–41.9			8.5–12.8	39.9			11.0
	EtOH	2	44.7–52.4			7.8	48.6			7.8
NL										
1.00–2.99	Formalin	6	38.5–50.8	19.6–23.0	19.1–24.0	12.8–16.3	44.6	21.7	20.7	15.1
	EtOH	5	38.4–50.0	17.9–21.2	17.5–23.8	9.3–14.7	43.2	19.6	20.2	12.0
3.00–3.99	Formalin	10	43.7–54.6	19.6–28.8	22.8–31.3	15.2–20.3	49.1	24.2	26.7	18.0
	EtOH	3	45.6–48.1	24.1–27.6	27.6–31.4	15.1–20.5	47.0	25.5	28.9	17.8
4.00–5.50	Formalin	5	39.0–51.8	21.2–30.4	23.2–37.4	16.3–20.7	45.8	25.0	30.6	18.4
	EtOH	3	36.5–50.1	23.7–31.7	30.6–46.4	18.4–21.1	45.3	28.1	36.6	19.4
FL										
4.50–5.99	Formalin	4	46.4–51.6	27.6–33.9	33.9–42.3	17.7–20.9	47.8	30.5	38.9	19.6
	EtOH	3	48.6–55.7	29.1–37.6	46.0–47.5	21.0–22.1	51.2	34.8	46.5	21.4
6.00–6.99	Formalin	3	44.6–48.0	25.0–28.4	30.2–39.5	15.2–16.0	45.7	26.7	36.1	15.7
SL										
6.00–6.99	Formalin	8	40.2–50.7	28.7–35.9	44.6–53.8	16.8–19.4	47.0	31.9	48.2	18.0
7.00–7.99	Formalin	10	42.9–51.5	30.5–33.9	42.7–54.2	15.7–18.4	47.0	32.3	47.5	16.9
8.00–8.99	Formalin	10	38.5–48.1	30.8–33.3	40.9–49.4	15.1–18.0	44.0	32.2	45.1	16.6

Table 5

Meristics of *Xystreurys liolepis* based on double-stained larvae.

		Fins						
Length	Vertebrae	Dorsal	Anal	Caudal	Pelvic	Pectoral	Branchiostegals	Gill raker
3.7 mm NL	–	–	–	–	–	Bud	–	–
3.9 mm NL	–	–	–	–	–	Bud	3	–
4.3 mm NL	–	–	–	–	–	Bud	2	–
4.4 mm NL	–	4	–	4	–	Bud	5	–
5.1 mm NL	–	4	–	2	–	Bud	4	–
5.1 mm FL	4 + 15	5	–	8	Bud	Bud	6	–
5.6 mm FL	11 + 26	63	55	8 + 8	4	Bud	7	4
6.7 mm SL	11 + 27	75	60	9 + 8	5	Bud	7	5
7.5 mm SL	11 + 26	71	57	10 + 8	6	Bud	7	5
8.4 mm SL	11 + 26	78	58	10 + 8	6	Bud	7	5

in the ventral finfold towards the end of the stage (Fig. 7E). Pigment is present on the elongate dorsal fin rays of flexion larvae and in the medial finfolds and fin anlagen in an area between about one-half and three-quarters the distance from snout to tail tip. Melanophores are also found at the anteriormost portion of the anal-fin anlage (Fig. 8A). Postflexion larvae are pigmented on the elongate dorsal fin rays, between about the 30th and 50th dorsal elements, and along most of the length of the medial fin bases. Melanophores are also present on the first few rays and near the midpoint of the anal fin (Fig. 8C).

Yolksac larvae are heavily pigmented at the tail tip with a few other melanophores found on the head and body (Figs. 7A, B). Scattered rows of dorsolateral and ventrolateral pigment form on the trunk and tail in the preflexion stage, but pigment along the dorsal and ventral margins does not form continuous double rows (one on either side of the margin) until late in the preflexion stage (Figs. 7D, E). Heavy dorsal midline

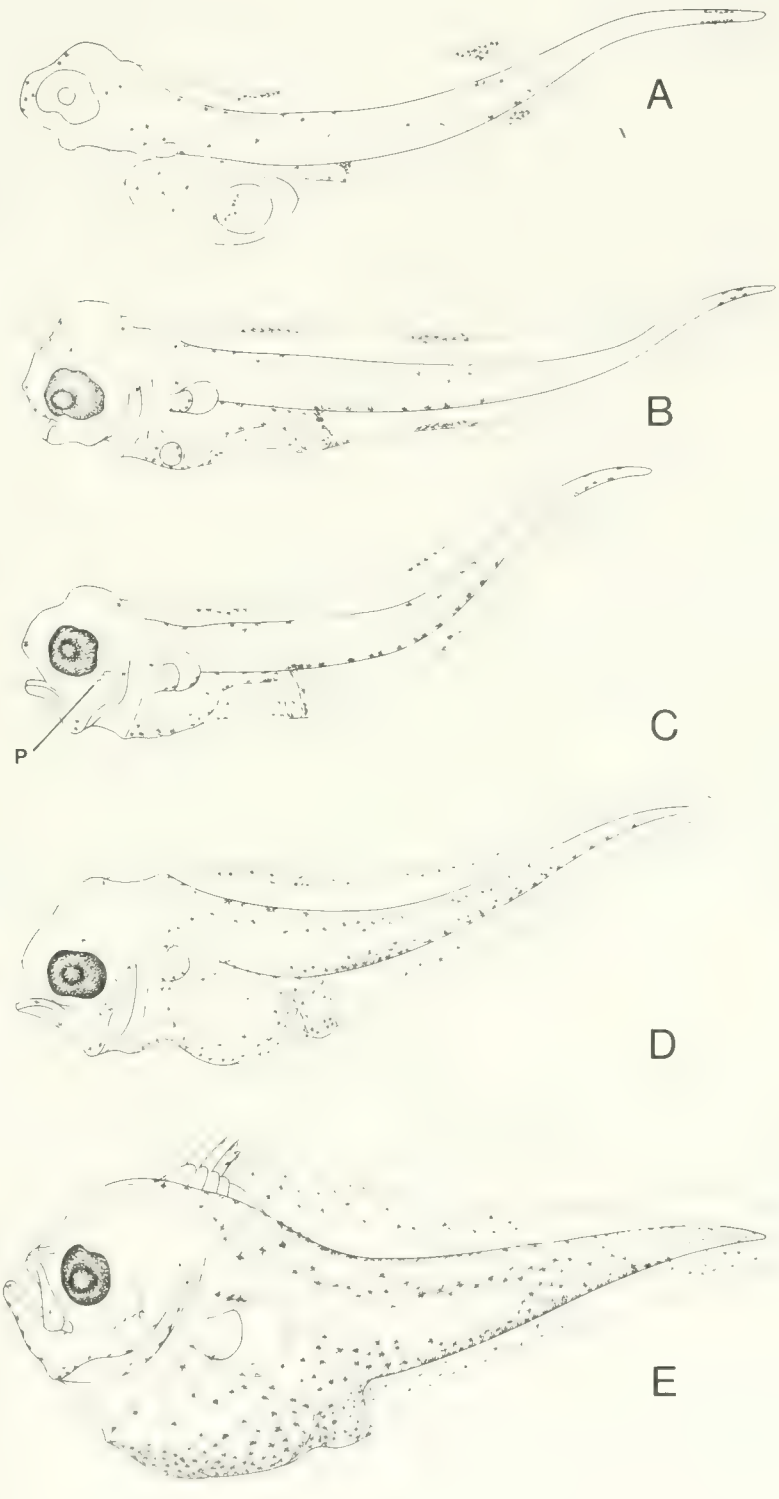

Figure 7

Xystreurys liolepis larvae (P = preopercular spines): (A) 2.0 mm YS (LACM 044 OB 15 OB 02P), (B) 2.1 mm YS (050 87 22 OB 02S), (C) 2.2 mm NL (LACM 044 87 36 OB 02S), (D) 2.8 mm NL (LACM 044 OB 22 OB 01S), (E) 4.2 mm NL (LACM 050 87 22 OB 02S).

and scattered dorsolateral melanophores of flexion larvae extend from about the first to the 29th or 30th myomere. Ventrolateral melanophores are located from approximately the 10th to the 30th myomere, and concentrated pigment along the postanal ventral margin is found from the vent to the last myomere (Fig. 8A). Dorsolateral and ventrolateral melanophores spread over the trunk and tail of postflexion larvae on all but the last six to eight myomeres, and several dense melanophores form posteriorly along the lateral midline (Figs. 8B, C).

Internal melanophores form on the dorsal surface of the notochord during the preflexion stage, but this pigment is obscured by thick musculature and heavy external pigmentation.

Pigment typically is present along the peritoneum and ventral midline of the gut at the end of the yolksac period. The gut of late-stage preflexion larvae is heavily pigmented, especially along the ventral margin from the cleithrum to the anus (Fig. 7E). Ventral margin pigment extends anterior to the cleithra in postflexion larvae (Fig. 8B).

Yolksac and preflexion larvae have few melanophores on the head and snout. Pigment develops on the upper and lower jaws, and upper palate of flexion stage larvae.

Larval comparisons Myomere or vertebral counts (34–36, *Paralichthys californicus* and 37–39, *Xystreurys liolepis*) will separate the larvae of *P. californicus* and *X. liolepis*, but these counts can be difficult to make, especially on small or damaged specimens. Morphological and pigment characters that will facilitate separation of the larvae of the two species until metamorphosis are given in Table 6. Visiblity of internal notochord pigment is the primary character for separation of post-yolksac larvae. Presence of sphenotic spines and

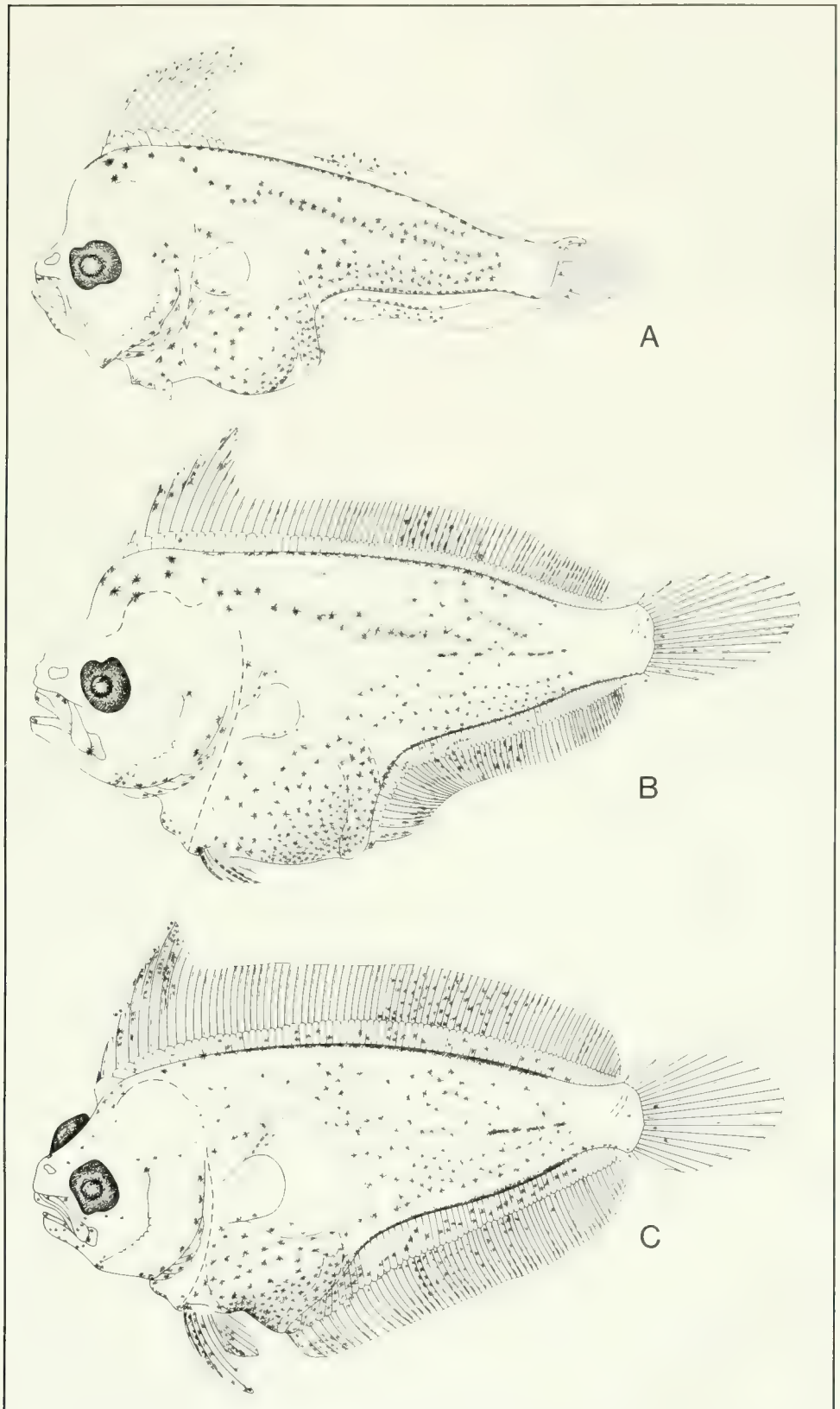

Figure 8

Xystreurys liolepis larvae: (A) 5.0 mm FL (LACM 051 88 36 OB 02P), (B) 6.3 mm SL (LACM 045 87 22 OB 01S), (C) 8.0 mm SL (LACM 037 OB 22 OB 02S).

Table 6

Comparison of larval characters: *Paralichthys californicus* and *Xystreurys liolepis*.

Paralichthys californicus (34–36 myomeres)	*Xystreurys liolepis* (37–39 myomeres)
Yolksac larvae (~2.0–2.5 mm NL)	
1. Sphenotic spines present	1. Sphenotic spines absent
2. Diffuse tail and finfold pigment	2. Concentrated patches of tail and finfold pigment
3. Many melanophores along the postanal ventral midline	3. Few melanophores along the postanal ventral midline
4. Late stage: Development of internal pigment along the notochord	4. Late stage: Internal pigment along the notochord obscured
Preflexion larvae (~2.5–4.5 mm NL)	
1. Presence of visible internal pigment along the notochord	1. Lack of visible internal pigment along the notochord
2. Sphenotic spines present	2. Sphenotic spines absent
3. Continuous row of postanal ventral midline pigment throughout the stage	3. Early to mid stage: Broken row of postanal ventral midline pigment
4. Mid to late stage: Body laterally compressed	4. Mid to late stage: Body robust
5. Mid to late stage: Row of external ventrolateral melanophores and external pigment at ~3/4 body length	5. Mid to late stage: Row of external dorsolateral and ventrolateral melanophores
6. Mid to late stage: Many ventral finfold melanophores	6. Mid to late stage: Few ventral finfold melanophores
7. Mid to late stage: Ventral midline pigment anterior and posterior to the cleithrum	7. Mid to late stage: Ventral midline posterior to the cleithrum
Flexion stage (~4.5–6.5 mm FL)	
1. Visible internal pigment along the notochord	1. Lack of visible internal pigment along the notochord
2. Body shape is laterally compressed	2. Body shape is robust
3. About 14 small gill rakers form on the first lower gill arch	3. About 4 gill rakers form on the first lower gill arch
4. Ventral finfold and anal fin anlage pigment along entire length	4. Ventral finfold and anal fin anlage pigment concentrated in patches
5. Ventrolateral row of trunk and tail pigment, little other lateral pigment	5. Dorsolateral and ventrolateral rows of trunk and tail pigment
6. Dorsal midline and lateral pigment extends to last myomere	6. Last 6–7 myomeres unpigmented laterally and along the dorsal midline
Postflexion larvae (~6.5–10 mm SL)	
1. Visible internal pigment along the notochord	1. Lack of visible pigment along the notochord
2. Body shape is laterally compressed	2. Robust body shape
3. Some external dorsolateral and ventrolateral pigment	3. Heavily pigmented externally
4. About 12–15 gill rakers on the first lower arch	4. About 4–5 gill rakers on the first lower arch
5. Dorsal midline and lateral pigment extends to the last myomere	5. Last 6–8 myomeres unpigmented laterally and along dorsal midline
6. 66–76 dorsal fin rays and 49–59 anal fin rays	6. 73–80 dorsal fin rays and 57–62 anal fin rays

finfold pigmentation will distinguish yolksac larvae. The more compressed shape of *P. californicus* and the robust, heavily pigmented body of *X. liolepis* are important characters for preflexion through postflexion stages. Material is lacking in the LACM collections to evaluate metamorphosed individuals, but meristic counts (i.e., gill rakers, dorsal fin rays, and ventral fin rays) will serve to separate juveniles.

Descriptions of the two species are based on field-collected material, but reared material was also examined. Pigmentation patterns of yolksac larvae were similar in reared and field material for both taxa. Pigmentation of reared larvae was heavier than that of field material in post-yolksac larval stages. Differences between reared and field-collected larvae of *Paralichthys californicus* increased as development

proceeded (reared specimens of *Xystreurys liolepis* older than early preflexion were not available for study). Reared specimens of *P. californicus* usually reflected the characteristic pigmentation patterns described from the field material, but the melanophores occurred in greater numbers and typically were more dendritic and heavily expressed. The eyed side of reared late-postflexion *P. californicus* larvae was covered with large dendritic melanophores obscuring most of the pigmentation characteristic of the field-collected larvae; however, the patterns were visible on the blind side. Furthermore, it appeared that reared larvae acquired pigmentation characteristics at an earlier developmental stage than did their field-collected counterparts.

The larval stages of three other species of *Paralichthys*—*P. dentatus* (Smith and Fahay 1970), *P. microps* (Munoz et al. 1988), and *P. olivaceus* (Pertseva-Ostroumova 1961, Okiyama 1967)—have been described. Larvae of *P. dentatus* and *P. olivaceus* hatch, undergo flexion, and transform at larger sizes than *Paralichthys californicus*. Larval size at hatching and at eye migration are similar for *P. californicus* and *P. microps*. All four species share the development of approximately five elongate, pigmented dorsal rays. *Paralichthys olivaceus*, *P. dentatus*, and *P. californicus* develop a series of sphenotic and preopercular spines. Opercular spines, not reported for *P. dentatus*, are present on both *P. olivaceus* and *P. californicus*. (Sphenotic and opercular spines were not reported in the description of *P. microps*.)

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Abstract.– Shortbelly rockfish *Sebastes jordani* is an abundant species that could support a large commercial fishery off central California. Prior studies of shortbelly rockfish growth were based on age data obtained from scales or whole otoliths. We show that broken and burnt otoliths provide reliable ages that are substantially different than those derived from previous methods. This new information was used to update estimates of the von Bertalanffy growth curve parameters, the natural mortality rate, and potential yield. We found that shortbelly rockfish live for up to 22 years. Males grew more slowly and reached a smaller maximum size than females. Estimates of natural mortality from three predictive models ranged from 0.212 to 0.378 for males and 0.203 to 0.437 for females. Assuming M is 0.20–0.35 and using biomass estimates from hydroacoustic surveys, we estimated that potential yield in the Ascension Canyon–Farallon Islands area ranges from 13,400 to 23,500 metric tons.

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Age, Growth, and Potential Yield for Shortbelly Rockfish *Sebastes jordani*

Donald E. Pearson
Joseph E. Hightower
Tiburon Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
3150 Paradise Drive, Tiburon, California 94920

Jacqueline T.H. Chan
Tiburon Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
3150 Paradise Drive, Tiburon, California 94920
Current address: 200 Ewing Terrace Drive, San Francisco, California 94118

Shortbelly rockfish *Sebastes jordani* is an abundant species in California waters. In midwater trawl surveys of juvenile rockfish conducted off central California, shortbelly rockfish were far more abundant than any other rockfish species (Wyllie Echeverria et al. 1990). The biomass of shortbelly rockfish in the Ascension Canyon–Farallon Islands area was estimated from hydroacoustic studies (E. Nunnely, NMFS Alaska Fish. Sci. Cent., Seattle, WA 98115-0070, pers. commun., Jan. 1989) to be 295,000 metric tons (t) in 1977 and 152,700 t in 1980. These estimates are one to two times the estimated coastwide virgin biomass for widow rockfish *S. entomelas* (Lenarz and Hightower 1988), a species that supports a significant commercial fishery. Currently, there is no commercial or sport fishery for shortbelly rockfish, but interest in surimi production or a new method of bone softening of whole fish (Okada et al. 1988), combined with their high abundance, could lead to the development of a substantial commercial fishery. If a commercial fishery does develop, it will be important to have accurate life-history information for management purposes.

Previous studies of shortbelly rockfish life-history characteristics have been based on age data from scales (maximum age 10 years, Phillips 1964) or whole otoliths (maximum age 12 years, Lenarz 1980). However, studies of other rockfish species (Six and Horton 1977, Beamish 1979, Kimura et al. 1979, Chilton and Beamish 1982, Boehlert and Yoklavich 1984, Stanley 1986, Leaman and Nagtegaal 1987) have shown that ages obtained from those structures tend to be underestimates, and that broken and burnt or sectioned otoliths are a more reliable method for determining fish age. W. Lenarz (Tiburon Lab., NMFS Southwest Fish. Sci. Cent., Tiburon, CA 94920, pers. commun., Jan. 1989) indicated that surface ageing of shortbelly rockfish otoliths was difficult and felt that the ages could have been greater than reported. For that reason, the objective of this study was to update the estimates of age, growth, and potential yield of shortbelly rockfish, based on examination of broken and burnt otoliths.

Materials and methods

Adult shortbelly rockfish were captured occasionally in 1983–88 midwater trawl surveys designed to monitor the abundance of juvenile

rockfish (Wyllie Echeverria et al. 1990). Samples were also obtained from a 1980 bottom-trawl survey of demersal adult rockfish (Gunderson and Sample 1980), and a 1981 fishery development survey using a midwater trawl (Kato 1981). The cod-end mesh size for these surveys ranged from 0.4 to 1.5 inches, and fish ages 1 and older were vulnerable to the gear. Otoliths were collected from 2238 fish from 48 tows at various locations along the northern California–central Oregon coast (Table 1). Sagittal otoliths were removed, cleaned, and either stored dry or in ethanol until they could be examined.

Table 1

Number of trawl tows containing adult shortbelly rockfish by area and year. Numbers in parentheses indicate total number of fish in the samples.

Region	1980	1981	1982	1983	1986	1988
Cape Blanco to Newport, OR	2 (175)	2 (100)		3 (130)		
Point Arena	1 (54)	1 (18)				
Farallon Islands		1 (49)			1 (107)	
Pescadero	1 (108)	2 (10)				2 (60)
Ascension Canyon	6 (423)	3 (147)	3 (152)	1 (126)	2 (91)	2 (101)
Monterey						2 (97)
Point Sur		13 (630)				
Total	10 (760)	21 (954)	3 (152)	4 (256)	3 (198)	6 (258)

Following Kimura et al. (1979) and Lenarz (1987), we examined the edges of broken and burnt otoliths collected from all months to determine whether marks formed on an annual basis. We attempted to get at least 100 fish per month (pooled over years); however, sample sizes were less than 100 for February, August, September, October, and December (Fig. 1). The broken and burned otoliths were examined without knowledge of sex, length, or date of capture. A dark burned edge was classified as winter growth; otherwise, the edge type was classified as summer growth. A few otoliths that appeared to be from older fish, for which edge type could not be identified clearly, were omitted from the study. Percent frequency of summer growth was plotted against month to examine periodicity in the formation of marks.

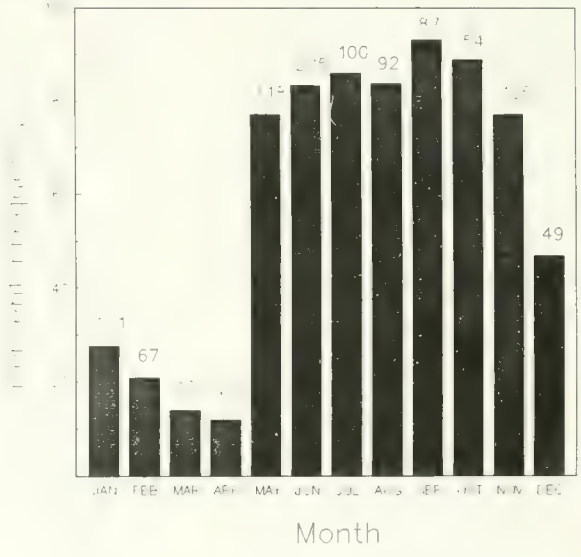

Figure 1

Frequency of light-colored edges (rapid growth period) for broken and burnt otoliths from shortbelly rockfish by month. Sample sizes are shown above each bar.

We used between- and within-reader comparisons to evaluate the consistency of broken and burnt otolith readings. To evaluate between-reader agreement, two readers independently examined a random subsample of 200 otoliths. To evaluate within-reader agreement, a random subsample of 200 otoliths was read twice, independently, by one reader. To compare ages obtained by otolith surface versus broken and burnt otoliths, one reader obtained ages for a random subsample of 200 otoliths, first from the surface and then independently from the broken and burnt halves.

We used the von Bertalanffy growth equation (Ricker 1975) to relate length and age:

$$L_t = L_\infty (1 - e^{(-k(t - t_0))})$$

where L_t = total length (mm) at age t,
L_∞ = estimate of average maximum length attained,
k = growth completion rate,
t_0 = theoretical age when fish is length 0.

Parameter estimates were obtained using nonlinear regression analysis (SAS Institute Inc. 1987). Growth equations were fitted separately for males and females and compared using the Extra Sum of Squares Principle (Draper and Smith 1981, Ratkowsky 1983).

To calculate potential yield, we estimated natural mortality (M) using several methods: (1) a regression equation relating maximum observed age and total mortality (Z, which equals M in this case) (Hoenig 1983); (2) an exponential model, in which the estimate of Z was based on both maximum observed age and sample size (Hoenig 1983); and a regression equation relating M to water temperature, average maximum length,

and growth completion rate (Pauley 1980). We used mean annual temperature for Ascension Canyon at a depth of 200 meters (8°C, Lynn et al. 1982). We did not estimate M using a catch curve (Ricker 1975) because shortbelly rockfish size tends to increase with depth and latitude (Lenarz 1980). For that reason, our opportunistic samples would not be expected to produce an unbiased estimate of the true age distribution.

Results and discussion

Age and growth

The edge-type analysis of broken and burnt otoliths supported our interpretation that marks were formed annually, generally between December and April (Fig. 1). This was similar to the findings of Kimura et al. (1979) for yellowtail rockfish *S. flavidus* and one month earlier than for widow rockfish *S. entomelas* (Lenarz 1987).

Between- and within-reader agreement was higher for shortbelly rockfish than for other rockfish species. Between-reader agreement was 76% to the year and 87% within one year; within-reader agreement was 77% to the year and 95% within one year (Fig. 2). Using whole otoliths, Six and Horton (1977) reported between-reader agreement for yellowtail rockfish *S. flavidus* to be 24% to the year and 71% within one year. For canary rockfish *S. pinniger*, Six and Horton (1977) reported within-reader agreements of 37 and 21% to the year for whole and sectioned otoliths, respectively. The higher levels of agreement for shortbelly rockfish could be due in part to their relatively young age, as percent agreement declined with increasing age beyond about age 4 (Fig. 2).

The comparison between ages derived from examination of the otolith surface and from broken and burnt halves revealed a systematic bias for fish older than age 4. Ages obtained from the otolith surface tended to be less than ages obtained from broken and burnt otoliths (Fig. 3). Beamish (1979) and Stanley (1986) reported similar results for Pacific ocean perch *S. alutus*.

Shortbelly rockfish live substantially longer than previously reported. The oldest fish we found was 22 years old as opposed to the previous estimate of 12 years (Lenarz 1980). There have been similarly large revisions in estimated maximum age of commercially important groundfish species off the west coast of Canada (Beamish and McFarlane 1987). Only 2 of 23 species were estimated to have maximum ages less than 20 years, and 13 *Sebastes* spp. (not including *S. jordani*) had maximum ages ranging from 36 to 140 years (Beamish and McFarlane 1987).

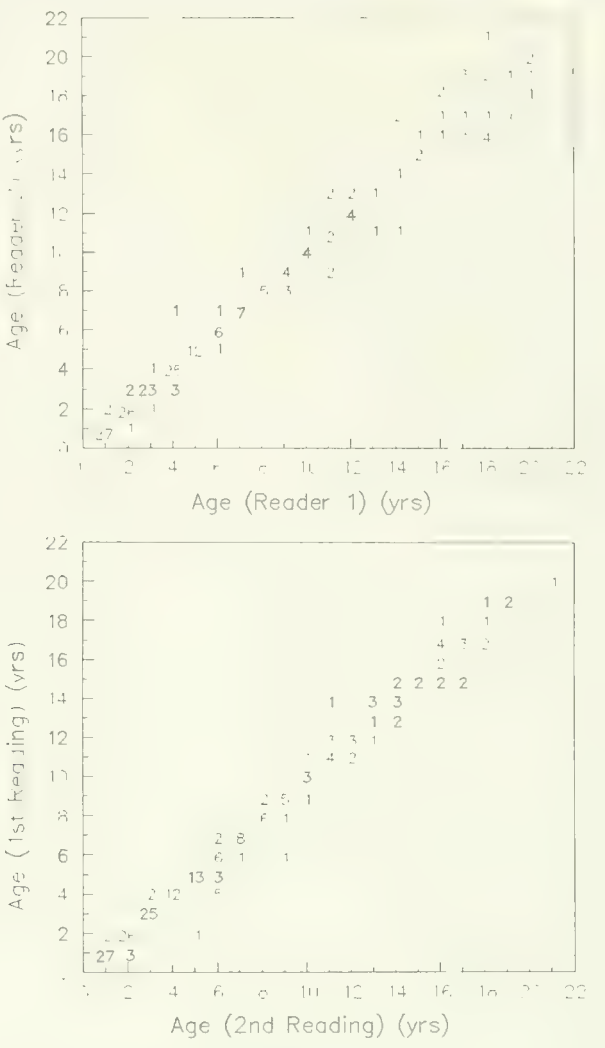

Figure 2
Between-reader (upper panel) and within-reader (lower panel) agreement for shortbelly rockfish ages determined from 200-fish subsamples using broken and burnt otoliths. Numbers at each point refer to number of otoliths examined.

Fitted growth curves differed significantly by sex, with males having a slower growth rate and a smaller maximum size ($F_{crit}(3, 1000, 0.01) = 3.80$, $F_{calc} = 115.23$) (Fig. 4). Although sample sizes were small, there was some evidence that the oldest females were smaller than somewhat younger females (Fig. 4). This could be due to shrinkage in older fish through senescence (Liu and Walford 1969); natural selection favoring small, older fish that use available energy for reproduction rather than continued growth (Leaman and Beamish 1984); or higher mortality for faster-

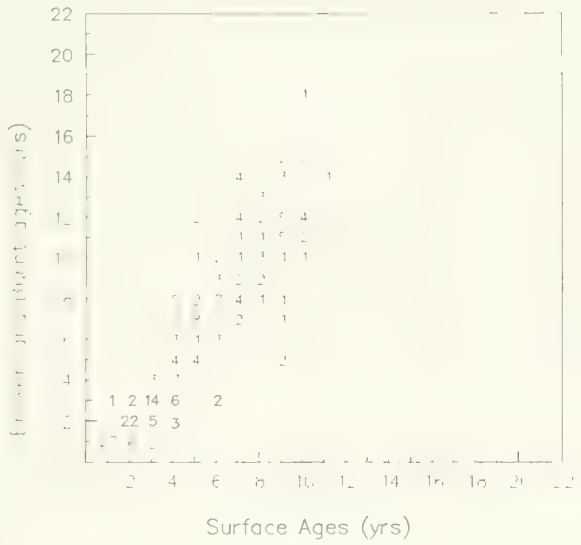

Figure 3
Shortbelly rockfish ages derived from broken and burnt otoliths and from surface readings of whole otoliths from a 200-fish subsample. Numbers at each point refer to the number of otoliths examined.

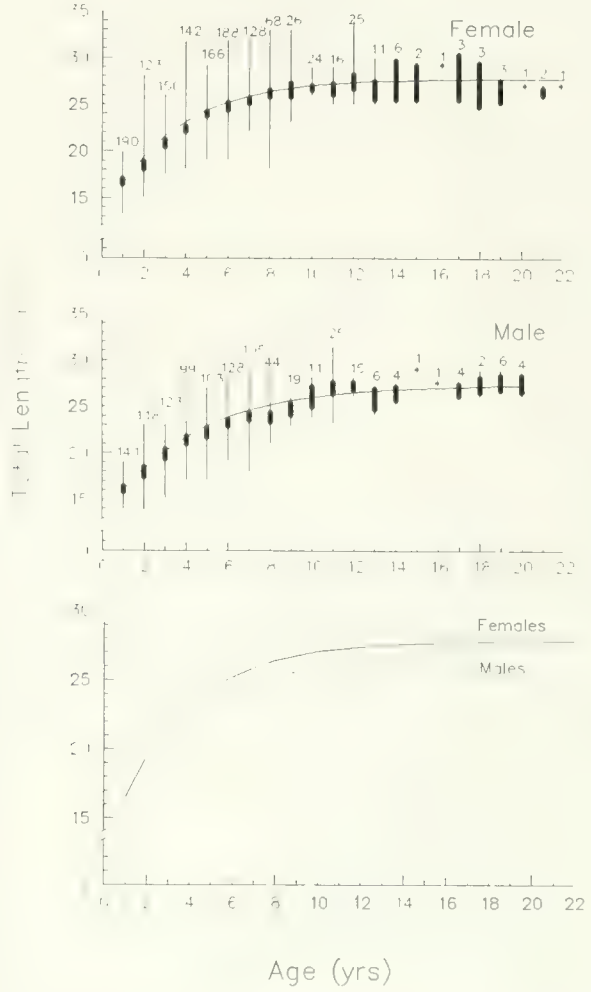

Figure 4
Mean length-at-age and fitted von Bertalanffy growth curves for male and female shortbelly rockfish (upper two panels) (range of values = thin line; 1 SE range = thick line, asterisks = length at which only a single fish was sampled; numbers above each line = sample size). The lower panel facilitates comparison of the sex-specific growth curves.

growing fish (e.g., due to size-selective fishing mortality). The same trend has been observed for yellowtail rockfish and Pacific ocean perch *S. alutus* (Leaman and Beamish 1984).

Our fitted von Bertalanffy growth curves (Table 2, Fig. 4) differed considerably from those reported by Lenarz (1980) and Phillips (1964). Our L_∞ values (Table 2) were lower than the estimates obtained from whole otolith ages (Lenarz 1980) or the combined-sex estimate obtained from scales (Phillips 1964). The decreases in L_∞ as maximum age increased are consistent with Hirschhorn's (1974) observation that a change in the range of ages used to fit the von Bertalanffy growth curve can result in changes to the parameter estimates. Wilson (1985) reported that use of the broken and burnt technique on *S. diploproa* and *S. pinniger* significantly altered von Bertalanffy parameter estimates. Our estimate of k for males was lower than that reported by Lenarz whereas the value for females was higher. The combined-sex estimate of k reported by Phillips (1964) was greater than either estimate obtained in this study. These differences in growth rate may be due to the increase in maximum age as well as differences in depths and areas sampled.

Table 2
Estimates of the von Bertalanffy growth parameters from scales, whole otoliths, and broken and burnt otoliths. Note: Phillips (1964) did not report separate values by sex; Lenarz (1980) did not report t_0 values.

Method	Sex	L_∞(mm)	t_0(yr)	k(yr^{-1})	Source
Scales	Combined	315	−0.270	0.275	Phillips (1964)
Whole otoliths	Male	290	—	0.298	Lenarz (1980)
	Female	324	—	0.211	
Broken and burnt otoliths	Male	279	−3.649	0.184	Present study
	Female	281	−2.514	0.253	

Natural mortality

Using Hoenig's (1983) regression equation, we estimated that M = 0.212 for males and 0.203 for females. We obtained higher estimates using Hoenig's (1983) exponential model (males 0.378, females 0.374) and Pauley's (1980) regression equation (males 0.356, females 0.437). Our sample sizes used in Hoenig's exponential model may have been overestimates (relative to true simple random samples from the population) because of the within-tow correlation. The effective sample size would probably be between 48 (the number of tows) and the number aged per sex (males 959, females 1279). Given the uncertainty of the above estimates, we assume that 0.20–0.35 is a reasonable range for M until a catch-curve estimate can be made. Catch-curve estimates for other *Sebastes* spp. from British Columbia waters were lower, ranging from 0.03 to 0.10 with a range of maximum observed ages from 32 to 77 years (Leaman 1986). Based on a catch-curve analysis, Lenarz and Hightower (1985) estimated that M for widow rockfish *S. entomelas* off Washington–Oregon–California ranged from 0.15 to 0.20. Lenarz (1984) reported that the maximum observed age for Washington-Oregon-California widow rockfish was about 45 years.

Potential yield

The historical estimate of maximum sustainable yield (MSY), 44,250 t, was based on the relationship MSY = $0.5MB_0$ (Gulland 1971), where B_0 was an estimate of virgin biomass (PFMC 1982). The MSY estimate was based on an assumed M of 0.275 and the 1977 survey estimate of Ascension Canyon to Farallon Islands area biomass (295,000 t) (E. Nunnely, NMFS Alaska Fish. Sci. Cent., Seattle, WA 98115-0070, pers. commun., Jan. 1989).

Our revised estimates of MSY were obtained from a more conservative model ($0.3MB_0$) that Gulland proposed because the former equation was thought to overestimate MSY (Gulland 1983). We used M = 0.20–0.35 and the average of the 1977 and 1980 Ascension Canyon to Farallon Island area biomass estimates (223,850 t). The revised estimates of MSY (13,431–23,504 t) should be viewed as highly preliminary, given that the 1977 and 1980 biomass estimates had confidence intervals in excess of 50% and were not significantly different.

The above estimates of MSY were based on the assumption that the fishing mortality rate (F) that produces MSY would be about equal to M. An alternative approach for obtaining a recommended F would be to determine the fishing mortality rate that reduced spawning biomass per recruit to 35% of the unfished level ($F_{35\%}$). That criterion is being used to manage most of the stocks in the Washington-Oregon-California groundfish fishery (PFMC 1990). Following Ricker's (1975) yield-per-recruit analysis, we calculated spawning biomass per recruit assuming M = 0.20 or 0.35 and linearly increasing maturity. Wyllie Echeverria (1987) reported that 50% of female shortbelly rockfish were sexually mature at age 2 and 100% at age 4. Those estimates were based on whole otolith ages; however, we found relatively good agreement between whole and broken-and-burnt otolith ages through age 4 (Fig. 3). The estimates of $F_{35\%}$ were similar to M if recruitment occurred at about age 2 (Fig. 5). Because shortbelly rockfish mature at a young age, estimates of $F_{35\%}$ increased considerably if recruitment was delayed. These results suggest that assuming F = M when calculating potential yield should provide protection for the spawning stock.

Our estimates of MSY for the Ascension Canyon to Farallon Island area are greater than the current (coastwide) acceptable biological catch (13,000 t) established to permit development of a fishery (PFMC 1989);

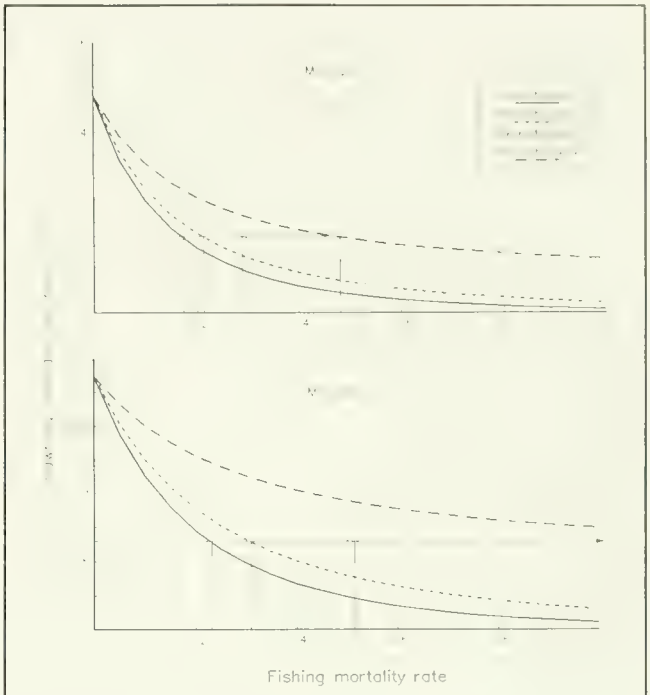

Figure 5

Female spawning biomass per recruit versus fishing mortality rate (F) at two levels of natural mortality (M) and four ages at recruitment. Horizontal lines represent spawning biomass per recruit equal to 35% of the level at F = 0; vertical lines represent the associated F ($F_{35\%}$). $F_{35\%}$ exceeds 1.0 for M = 0.35 and recruitment age of 4 years.

therefore, a change in acceptable biological catch does not appear to be necessary to protect the stock. Estimates of shortbelly rockfish abundance (and potential yield) to the north and south of the surveyed area may not be feasible prior to development of a fishery. However, the limited data available suggest that other aggregations may exist. In a study of larval rockfish distributions from Baja California to Bodega Bay, California; MacGregor (1986) found that shortbelly rockfish larvae were most abundant in the Ascension Canyon to Farallon Islands area (49%). He also detected a large concentration in the Channel Islands off southern California (35%), suggesting the presence of a large number of adults in that area. Gunderson and Sample (1980) examined the distribution of pelagic adult rockfish from southern California to Vancouver, British Columbia. They found the highest concentration of shortbelly rockfish in the Ascension Canyon to Farallon Islands area but also detected concentrations in the Channel Islands, in the Point Sur area of California, and off Bodega Bay, California. A smaller concentration was found off the Columbia River in Oregon. These observations suggest that our estimates of MSY are conservative when applied coastwide. More refined estimates of potential yield should be possible once a fishery develops or once planned larval production surveys of the Ascension Canyon to Farallon Islands area have been conducted.

Acknowledgments

We thank Thomas Laidig, Bruce Leaman, William Lenarz, Milton Love, and Stephen Ralston for their valuable critiques of this manuscript.

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Abstract. – Variation in color pattern, dorsal fin shape, and body length exhibit sharp north/south gradients centered at about 5–10°N latitude and east/west gradients at about 120–125°W longitude. A conservation zone with boundaries in these regions would provide protection for the morphologically unique eastern spinner dolphin *Stenella longirostris orientalis*. A radial pattern of geographic variation in the eastern Pacific and a complex pattern of discordant variation outside the core range of *S. l. orientalis* suggest that the present separate management of "whitebelly" spinner dolphins (which comprise a broad zone of hybridization/intergradation between *S. l. orientalis* to the east and the pantropical spinner dolphin *S. l. longirostris* to the west and southwest) north and south of the Equator may not be justified on the grounds of conservation of distinct populations.

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Geographic Variation in External Morphology of the Spinner Dolphin *Stenella longirostris* in the Eastern Pacific and Implications for Conservation

William F. Perrin
Priscilla A. Akin
Jerry V. Kashiwada

La Jolla Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271, La Jolla, California 92038-0271

Spinner dolphins in the eastern tropical Pacific vary geographically in color pattern (Perrin 1972), in external and skeletal size and shape (Perrin 1975, Perrin et al. 1979a, Schnell et al. 1982 and 1985, Douglas et al. 1986), and in reproductive seasonality (Barlow 1984). Perrin (1975) and Perrin et al. (1979a) described several forms that have served as stock units for management of populations of dolphins killed incidentally in the international purse-seine fishery for yellowfin tuna in the region (Perrin et al. 1985). Kills in recent years have been on the order of 100,000 annually. The management units have been known as the "Costa Rican," "eastern," "northern whitebelly," and "southern whitebelly" spinner dolphins. The geographic ranges of the eastern and whitebelly forms overlap broadly (Perrin et al. 1985).

The model used in studies and, to a lesser degree, management of the species in the region has been one of several discrete, more-or-less reproductively isolated stocks with some geographic overlap. However, as more morphological data have accumulated, a different picture has emerged. For example, while the boundary between the present northern and southern whitebelly management stocks was drawn latitudinally, the overall pattern of variation in the eastern Pacific now appears radial (Schnell et al. 1982 and 1985, Perrin et al. 1985). Further, the results of a genetic study indicate substantial exchange of at least mitochondrial DNA between and among the eastern and whitebelly forms (Dizon et al. 1991). Most recently, Perrin (1990) described two subspecies, *Stenella longirostris centroamericana* and *S. l. orientalis*, based on the Costa Rican and eastern forms, respectively, and concluded that the whitebelly "forms" (Fig. 1) collectively comprise a broad zone of intergradation or hybridization between the eastern subspecies and a third subspecies to the west and southwest, the pantropical spinner dolphin *S. l. longirostris*, a form occurring in the central and western Pacific, Indian and Atlantic Oceans (Perrin et al. 1981; Gilpatrick et al. 1987).

In this context, the purpose of the present study was to reexamine variation in external morphology on a finer geographical scale than had been used in earlier studies. Specimens previously identified as "Costa Rican," "eastern", or "whitebelly" based on the modal appearance of adult animals in the schools from which they came were pooled in the analyses. In this way we hoped to

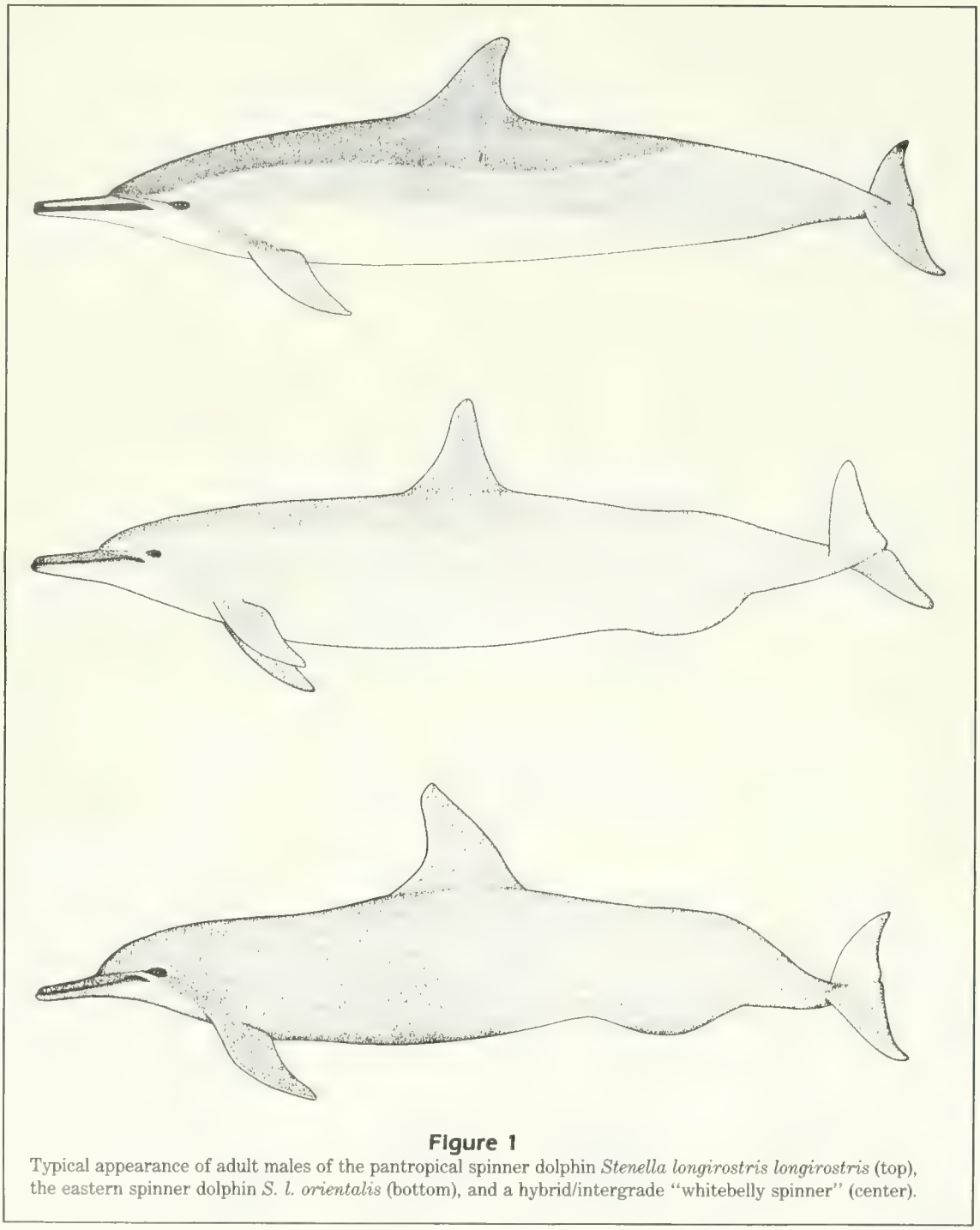

Figure 1
Typical appearance of adult males of the pantropical spinner dolphin *Stenella longirostris longirostris* (top), the eastern spinner dolphin *S. l. orientalis* (bottom), and a hybrid/intergrade "whitebelly spinner" (center).

gain a better understanding of the morphological gradients and other geographical patterning involved in the relationships among the Central American, eastern, and pantropical subspecies and to contribute to the development of approaches to conservation and management of the several populations.

Materials and methods

Source of the data

We examined variation in the ventral field and cape components of the color pattern (terminology of Perrin 1972), the shape of the dorsal fin, and body length.

The data on color pattern and dorsal fin were collected by biologists during the period 1974–88 aboard commercial tuna seiners (see Acknowledgments). The length data were collected in 1968–89. The biologists completed a field "life-history" form for each dead dolphin examined, recording basic information such as sex and length and (starting in 1974) sketching in the ventral field, cape (if prominently visible; see below), and dorsal fin on a preprinted generalized dolphin outline. When feasible, the observer also traced the dorsal fin on the back of the data form. Body length was measured to the nearest cm with calipers mounted on a 2-m wooden ruler. For male specimens, a testis with epididymis attached was preserved and weighed ashore. For females, the number of corpora in the ovaries was determined in the laboratory (methods described in Perrin et al. 1976).

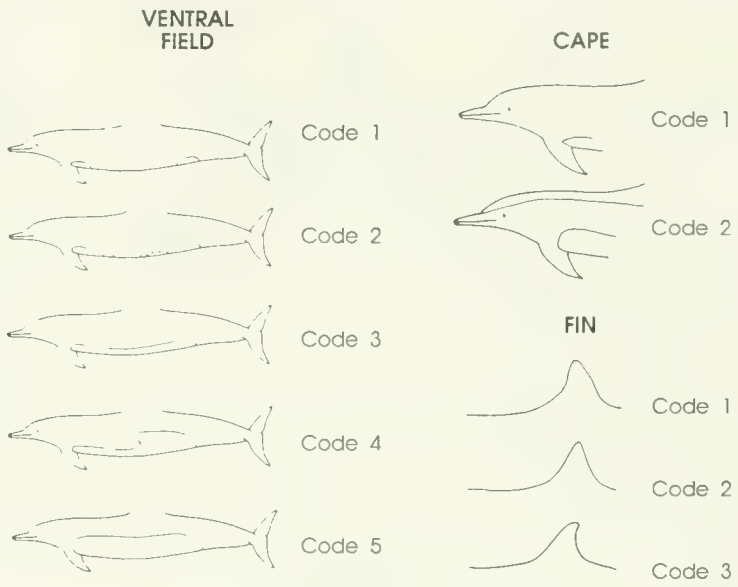

Figure 2
Character states for coding of ventral field, cape, and dorsal fin in spinner dolphins.

The quality of the sketches varied greatly. Although a few color pattern sketches were discarded as totally unusable, the basic features of the color pattern could be discerned in relatively inexpert sketches. However, the fin sketches proved to be unreliable. We found that for the cases where the observer both sketched and traced the dorsal fin, the correspondence between fin shape in the sketch and tracing was often poor. Therefore we used only the fin tracings, which reduced the sample size for dorsal fin shape. We also examined photographs of the specimens if they were available.

The analyzed data consisted of body length in cm and coded values for ventral field, cape, and dorsal fin shape. These were accompanied by date and location of capture and reproductive data (weight of testis + epididymis for males; number of ovarian corpora for females).

The ventral field received a code from 1 to 5 (Fig. 2). Code 1 is the state typical of the eastern subspecies; Code 5 is that typical of the pantropical subspecies (Fig. 1). Codes 2–4 are intermediate. In Code 1, the animal is gray laterally and ventrally, with white patches in genital and axillary regions. In Code 2, the separate genital and axillary white areas of Code 1 are joined by a speckled zone. In Code 3, the two areas are confluent, forming a white ventrum. In Code 4, the ventral field extends dorsally above the umbilical-genital region, yielding a stepped pattern in lateral view. In Code 5, the anterior portion of the ventral field extends dorsally to behind the eye, eliminating the step of Code 4. This variation is continuous, of course; a code was assigned for the state closest to that evident in the sketch. The sketches themselves already incorporated some artificial stratification. For example, in some animals the darker region yielding the step of Code 4 is only faintly evident. Some observers indicated the presence of this faint feature, leading us to code the animal as Code 4; others undoubtedly overlooked such faint markings or failed to record them, leading us to code the animals as Code 5. While such errors could be expected to blunt the resolving power of the analyses, there is no reason to suspect that they inject a systematic spatial bias that would affect the accuracy of the conclusions; the data were collected by a large number of observers working over large areas.

The cape (Fig. 2) was coded as "not noted in the sketch" (Code 1) or "noted in the sketch" (Code 2). In a living or freshly dead spinner dolphin, the cape can be discerned on close and careful inspection, if only very faintly, in all cases. In the eastern spinner, the dorsal overlay (terminology of Perrin 1972) is very dense, almost obliterating the underlying cape in even very fresh specimens. When a carcass of an eastern spinner has lain on the deck of a tuna boat for more than a few minutes, the dorsal overlay darkens to the point of completely obscuring the cape. In the live pantropical spinner, the dorsal overlay is less dense and the cape is sharply defined and obvious. It is detectable even in specimens dead for several hours, albeit more faintly. Thus the absence of the cape in a sketch means that the observer did not note it upon fairly cursory

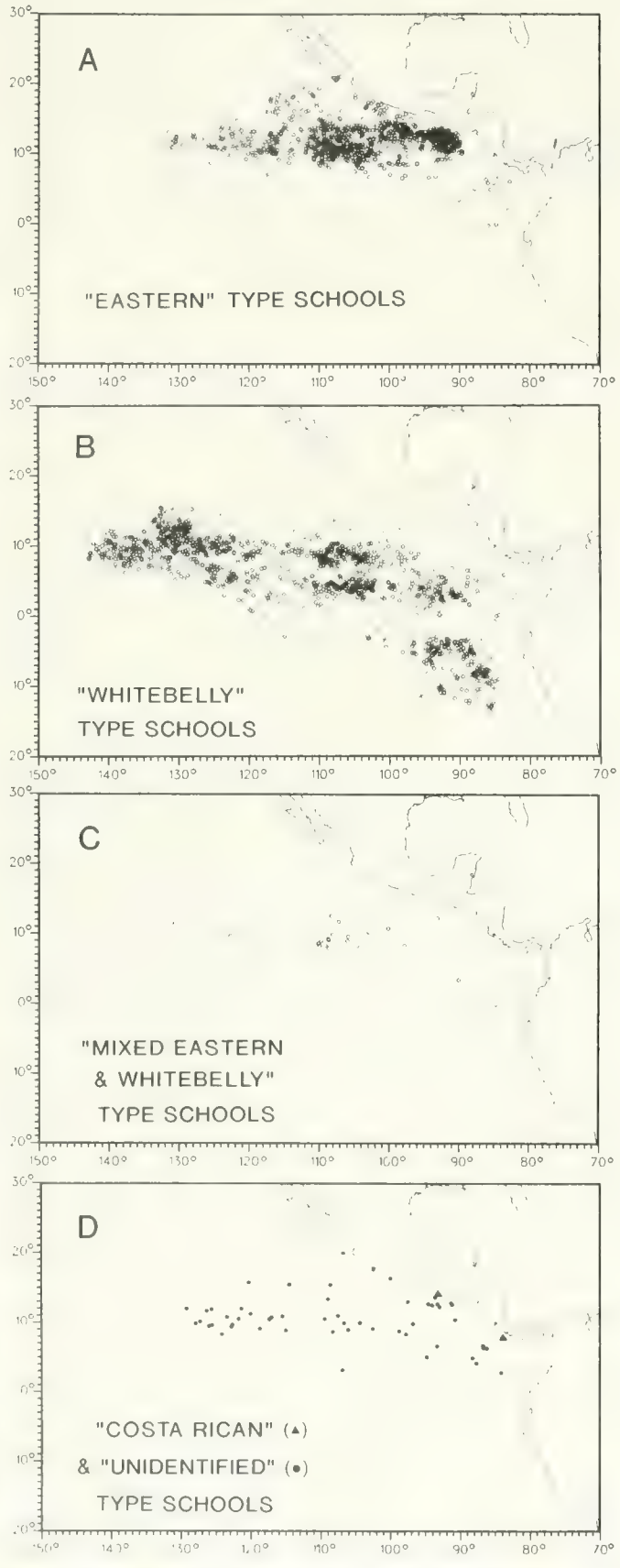

Figure 3
Localities for purse-seine sets on schools of spinner dolphins for samples included in analyses, by school type (see text for school-identification criteria).

inspection, not that it was not actually absent. Cape "presence" is a relative measure of the density of the dorsal overlay, with some precision lost due to post-mortem darkening. Again, under the assumption that time before examination of the carcasses and diligence of the observers did not vary with area, there should be no systematic bias.

The dorsal fin was coded to one of three states (Fig. 2): canted—closest to a right triangle with hypotenuse posterior (Code 1; most "eastern-like"), erect—isosceles triangle (Code 2), or falcate—right triangle with hypotenuse anterior (Code 3; most "pantropical-like"). Sources of error in this code include partial tracings of fins (part of the base of the fin not included) and injuries distorting the fin. The first was difficult to cope with and could not be resolved completely. Some tracings were discarded because of sharply anomalous shape obviously due to the fin being incomplete, but some small portion of the variation recorded is undoubtedly due to undetected errors of this sort. When a distal portion of the fin was missing due to injury, this was indicated in the observer's sketch, and the tracing was not used. The tracing was also not used if a very large notch or gap was indicated. Small notches and holes do not affect the overall shape of the fin.

The total of the code scores for the three characters ranged from 3 (typical of the adult male eastern spinner) to 10 (typical of the adult male pantropical spinner).

The sample

The sample for color pattern and fin shape included 8350 specimens from 971 net sets on "eastern"-type schools, 1200 sets on "whitebelly"-type schools, 27 sets on "mixed eastern and whitebelly" schools, 2 sets on "Costa Rican"-type schools, and 54 sets on spinner dolphins of unidentified stock (Figs. 3 and 4). Not all

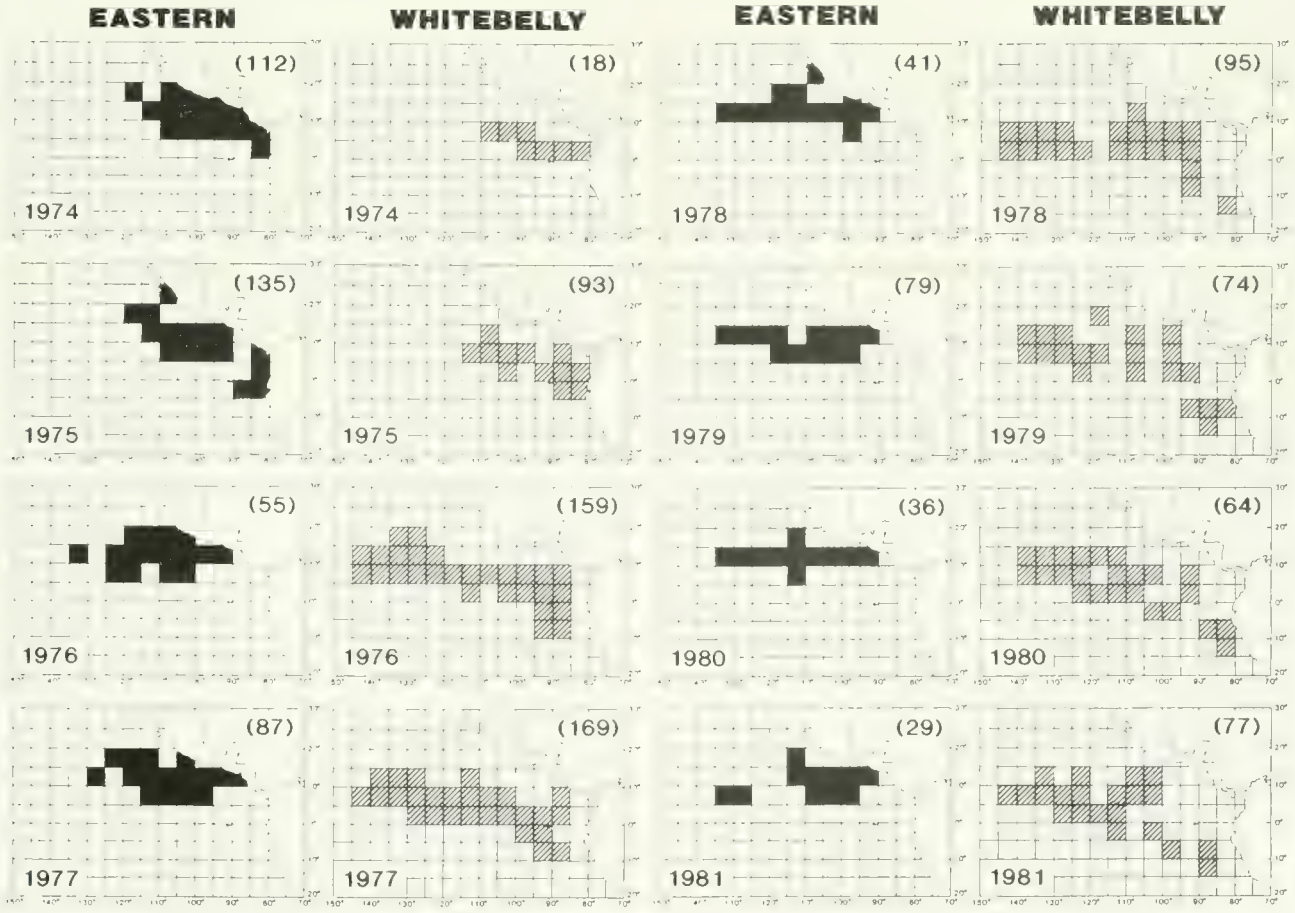

Figure 4

Distribution, by year, of purse-seine sets on "eastern" and "whitebelly" schools of spinner dolphins for samples included in analyses.

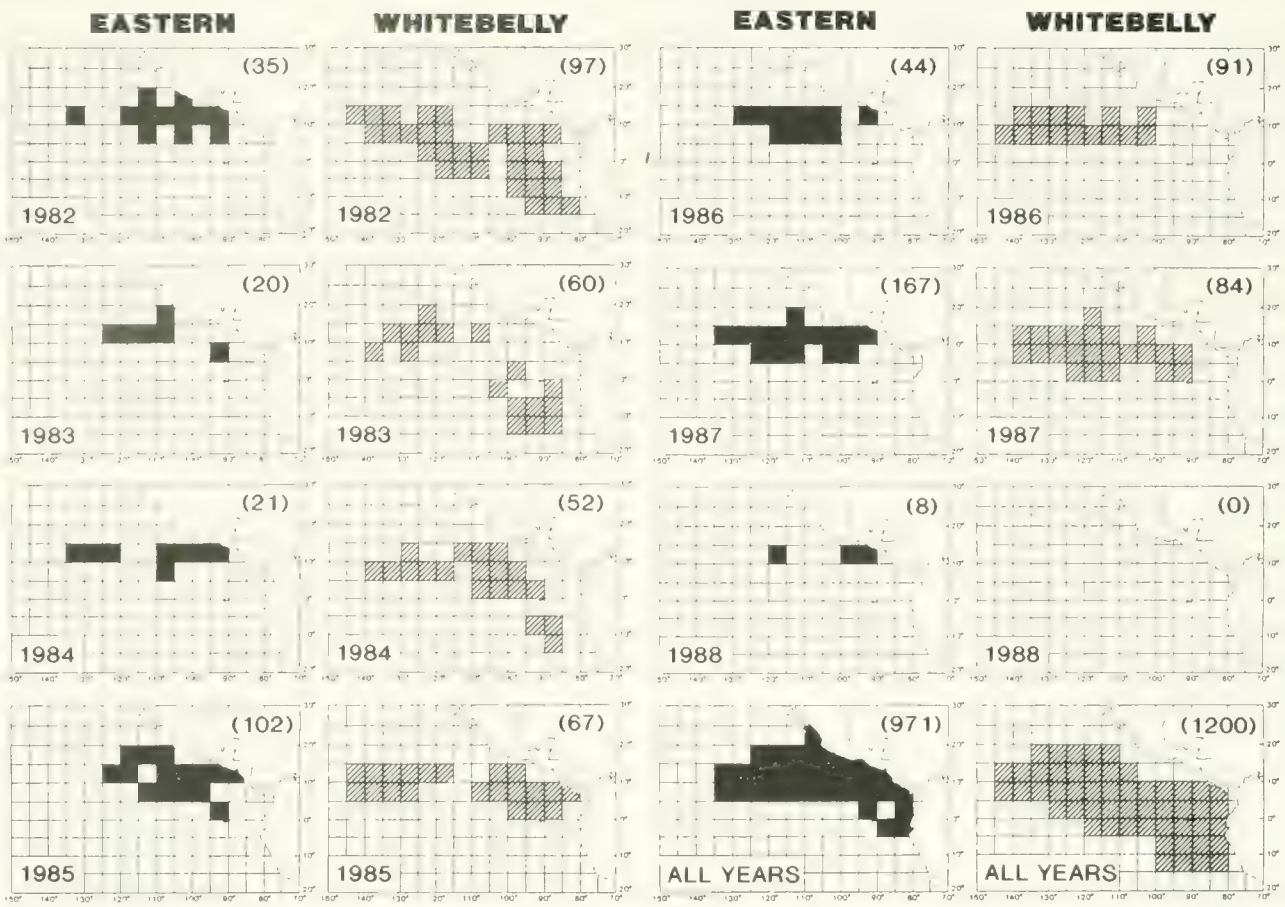

Figure 4 (continued)

of the characters were recorded for all of the specimens (Table 1). Body-length data were available for 3304 adult dolphins (1461 males and 1843 females). (Females with at least one ovarian corpus and males with testis/epididymis weight of 100g or more were considered adult, following Perrin et al. 1977.)

Table 1
Sample sizes for analyses of color pattern and fin shape of spinner dolphin in the eastern tropical Pacific Ocean.

Character	Males	Females	Total
Total individuals	4121	4229	8350
Ventral field	3377	3463	6840
Cape	3376	3462	6838
Fin shape	2053	2421	4474
Adults with all 3 characters	610	683	1239

Analytical methods

Areal stratification For purposes of the analyses, we divided the study area into 60 5-degree blocks with boundaries at the Equator, 5 degrees, 10 degrees, etc., and 80 degrees, 85 degrees, etc. We experimented with 4-degree blocks and with different placement of the boundaries but obtained less consistent results (more embedded and peripheral anomalous blocks) than with the scheme adopted.

Effects of sexual dimorphism and development Color pattern and fin shape are known to vary with sex or age or both (Perrin 1972). We endeavored to take into account these factors in the geographical analyses by considering males and females separately where necessary and by applying a minimum length or sexual-maturity criterion for specimens to be included in analyses of each of the characters separately.

Because they relate primarily to the methodology of the study, the results of analyses to establish the length/maturity criteria are presented here rather than below with the results of the analyses of geographical variation.

We found no difference between the sexes in extent of the ventral field but a statistically significant association between ventral field state and body length (contingency test of association with Peterson's chi-square, α 0.05; computer program BMDP4F in Dixon et al. 1990). As described by Perrin (1972), all calves tend toward the "whitebelly" color pattern (codes 4 or 5), with reduction in the ventral field in "eastern" spinners with age (to Codes 1, 2, or 3). The proportion in the overall present sample with Code-5 ventral field (most "whitebelly-like") declined with body length until about 120 cm, when it stabilized at about 30–35% (Fig. 5), and the proportion of individuals with Code 1 ventral field (most "eastern-like") behaved similarly but conversely. We therefore limited the analyses of ventral field to specimens of 120 cm or larger. (After about 170 cm, the proportion of Code-5 animals again climbed and Code-1 animals decreased; this is because most specimens above that length were "whitebelly" spinners—see analyses below of geographical variation in body length.)

Noted presence of the cape exhibited a similar pattern of change with growth (Fig. 6). Calves in all regions tend to exhibit a strongly defined cape, which is progressively obscured with development of the "eastern" pattern (Perrin 1972). Again, relative stability in the proportion of all animals for which the cape was noted was reached at about 120 cm in both sexes; the sample for the geographic analyses was limited to specimens of this length or greater.

We also found a slight association of expression of the cape with gender; the cape was noted for 10.1% of all females but only 7.8% of males (Fig. 6). In the geographical analyses, we used the average of male and female means in order to avoid effects of possible areal variation in sex ratio in the samples.

The degree of sexual dimorphism in the shape of the dorsal fin varies geographically, ontogenetically, and individually (Perrin 1972). In the present sample, in schools classified as "eastern" (Fig. 7), about 60% of small calves of both sexes had erect dorsal fins (Code 2); the balance had falcate fins (Code 3). Beginning at about 135 cm, erect fins increasingly predominated, to more than 80% in large juveniles of both sexes and about 90% in adult females. In males, the first canted fins (Code 1) appeared at about 160 cm. They increased in frequency to about 70% in large adults of 180 cm or more. This corresponds roughly to the length at which about 80% (the asymptotic level) have achieved at least minimum testis-epididymis weight (94 g) at which spermatogenesis occurs (Perrin and Henderson 1984). Thus, the canted fin in the eastern-type animals was strongly associated with sexual maturity, although some mature males had erect fins.

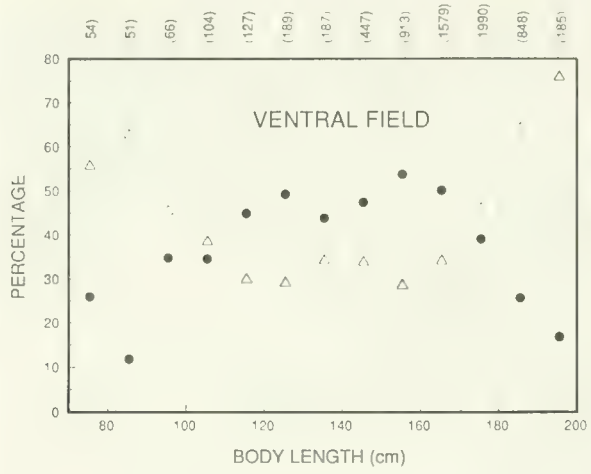

Figure 5

Change in ventral field in relation to body length in spinner dolphins. Circles are Code 1; triangles are Code 5. All specimens over 195 cm included in last interval. Sample sizes in parentheses (total 6840).

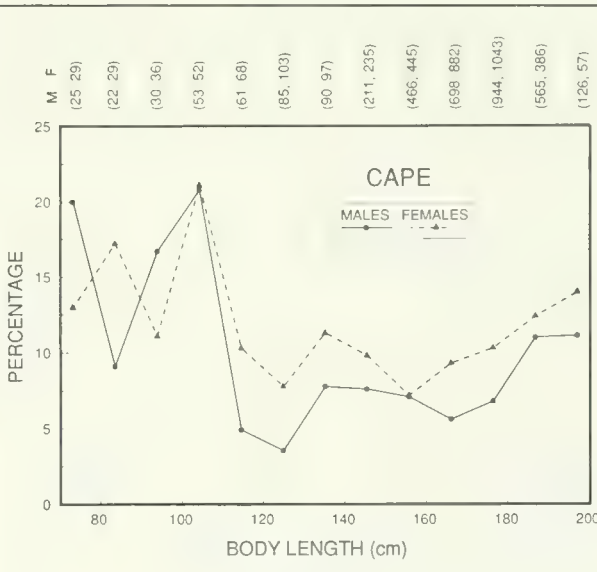

Figure 6

Change in percentage with noted cape in relation to body length in males and females. All specimens over 195 cm included in last interval. Sample sizes in parentheses (total males 3376, total females 3462).

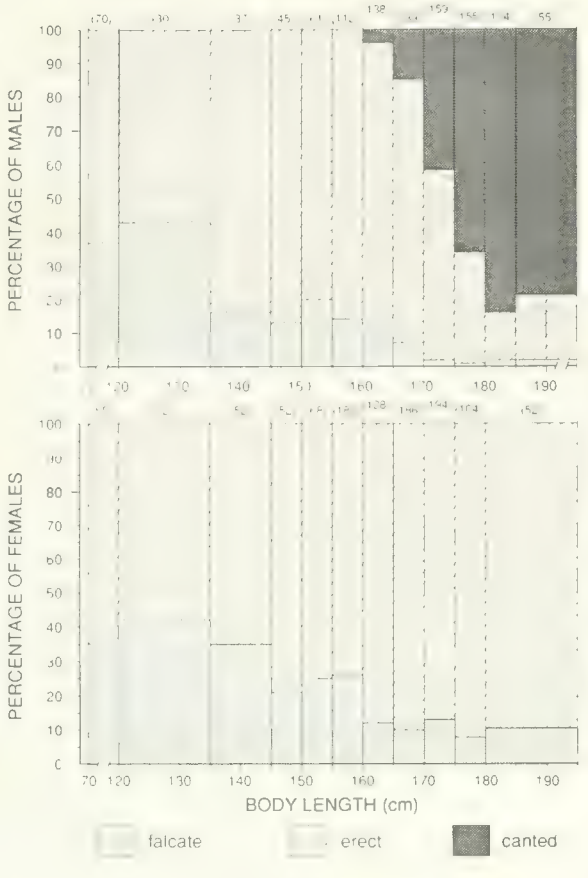

Figure 7
Change in percentage of males (top) and females (bottom) from "eastern"-type schools with canted (Code 1), erect (Code 2), and falcate (Code 3) dorsal fins in relation to body length. Sample sizes in parentheses.

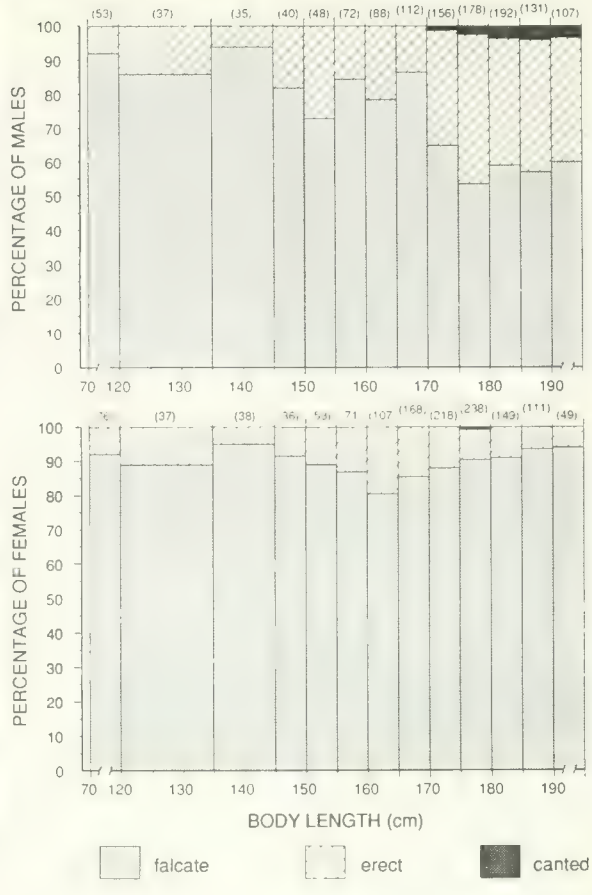

Figure 8
Change in percentage of males (top) and females (bottom) from "whitebelly"-type schools with canted (Code 1), erect (Code 2), and falcate (Code 3) dorsal fins in relation to body length. Sample sizes in parentheses.

In the "whitebelly" schools (Fig. 8), roughly 90% of calves, juveniles, and adult females had falcate dorsal fins and about 10% erect fins. One adult female had a canted fin. In adult males, the frequency of erect fins increased to about 40% in individuals of 175 cm or more (2.3% had canted fins). Again, this is about the length at attainment of sexual maturity (*loc. cit.*). We limited the analyses of dorsal fin shape in the pooled samples to sexually mature dolphins and considered males and females separately.

We followed the same procedure for analyses of body length, limiting the sample to sexually mature animals and analyzing males and females separately.

Effects of seasonal variation The apparent overlap of collection localities for the two kinds of schools is not an artifact of seasonal migrations. The region of substantive overlap of "eastern" and "whitebelly" schools is between 8° and 12°N and 95° and 125°W (Fig. 3). We examined the data by quarter of the year and found overlap in this region in all four quarters.

Pooling to obtain adequate sample sizes Sample sizes in many cases were very small for some of the peripheral 5-degree blocks. In these cases we pooled the samples over two or more blocks, to achieve a minimum sample size of 25. In the pooling we attempted to approximate the apparent radial pattern of variation, i.e., pooling was mainly longitudinal in the south and mainly latitudinal in the west. To the extent possible, we maintained the same pooling scheme from analysis to analysis, although in some cases differential pooling was required for males and females. The sample sizes and pooling schemes for the various analyses are given in the Appendix.

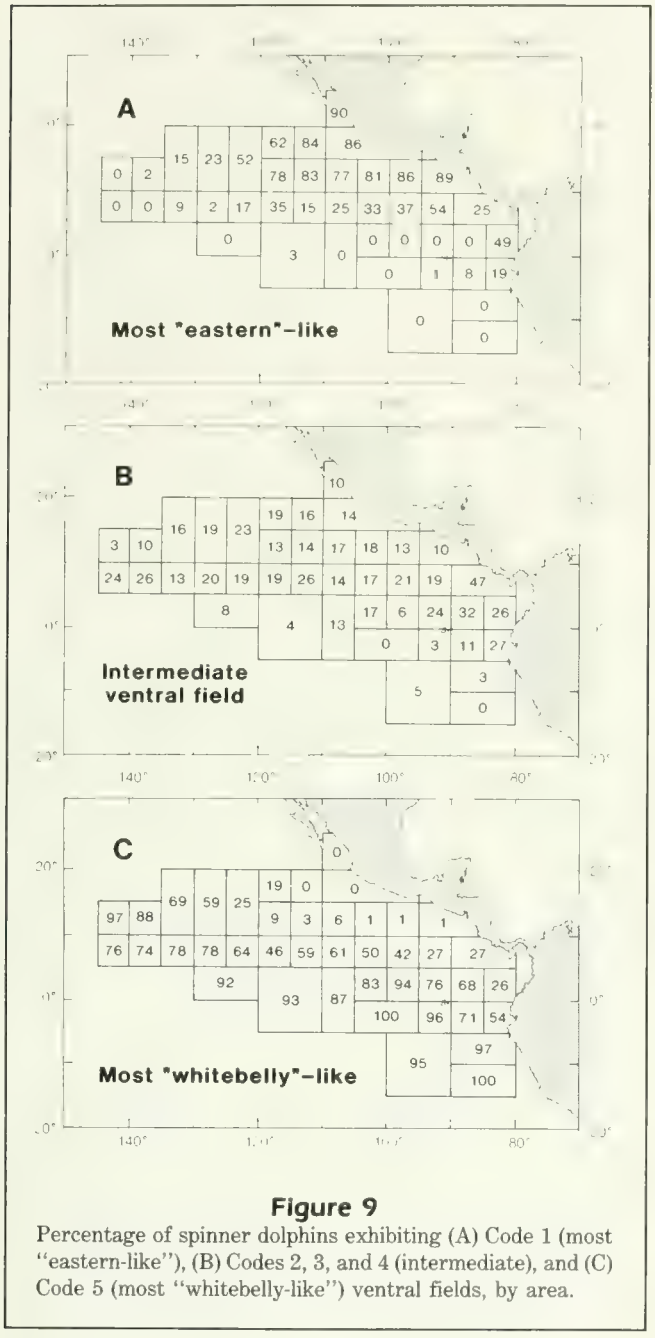

Figure 9
Percentage of spinner dolphins exhibiting (A) Code 1 (most "eastern-like"), (B) Codes 2, 3, and 4 (intermediate), and (C) Code 5 (most "whitebelly-like") ventral fields, by area.

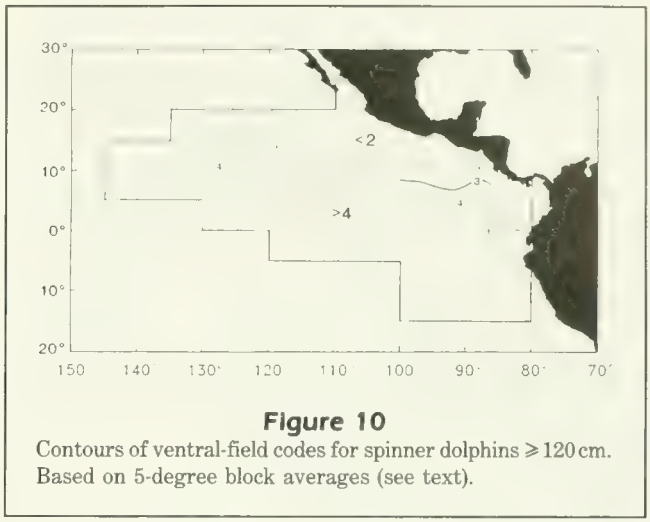

Figure 10
Contours of ventral-field codes for spinner dolphins ≥120 cm. Based on 5-degree block averages (see text).

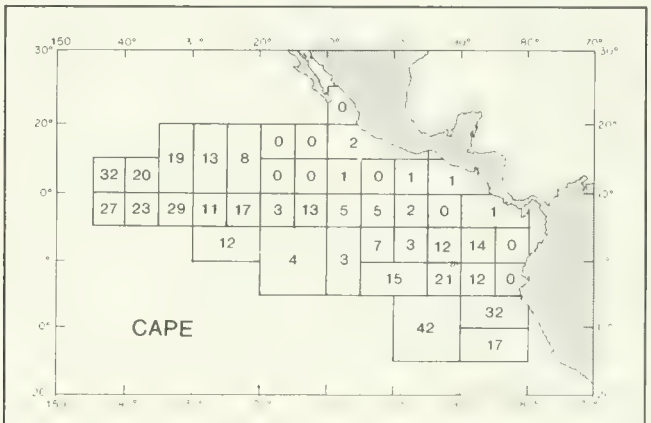

Figure 11
Percentage of spinner dolphins with observed cape, by area.

Contouring We used the ZSMTH, ZGRID, and ZCSEG subroutines of the PLOT88 graphics software package (Young and Van Woert 1987) to generate contours of ventral coloration scores for unweighted 5-degree blocks. The center of a block was used as the position for the mean ventral coloration score of specimens collected within the block. We used ZGRID with the "cay" parameter set at 5 and "nrng" set at 4 to generate a data grid for contouring. ZSMTH with "nsm" set at 1 was used to smooth the grid. Contour lines were generated using ZCSEG with "ndiv" set at 4.

Results

Ventral field

The pattern of disjunct axillary and genital white areas (Code 1) occurred at high frequencies (≥75%) in a relatively small part of the study area, in 12 5-degree blocks north of 10°N and east of 120°W (Fig. 9A). It was totally absent south of 5°S and absent from most of the peripheral blocks between 15°N and 5°S. It occurred at intermediate frequencies near Central America and northern South America, between 10°N and 5°S. The steepest gradient would appear to have been at about 10°N, extending from the coast out to possibly beyond 125°W. This pattern was mirrored in the relative distribution of the Code-5 ventral field (most "whitebelly-like"), which was absent or nearly absent from most of the northeastern blocks where the Code 1 pattern predominated and occurred at frequen-

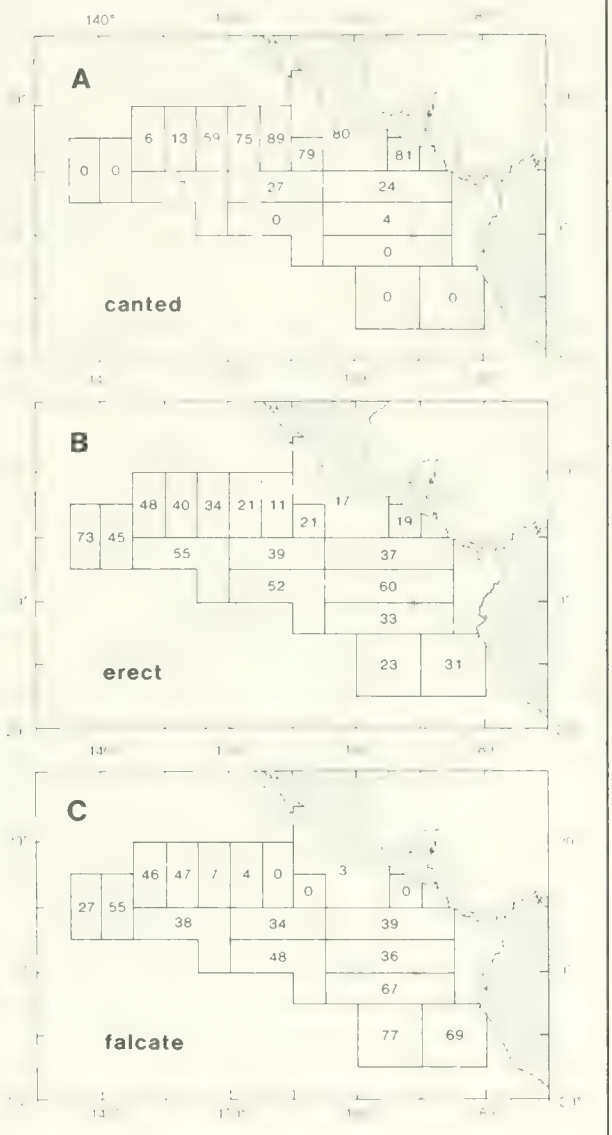

Figure 12
Percentages of adult male spinner dolphins with (A) canted, (B) erect, and (C) falcate dorsal fins, by area.

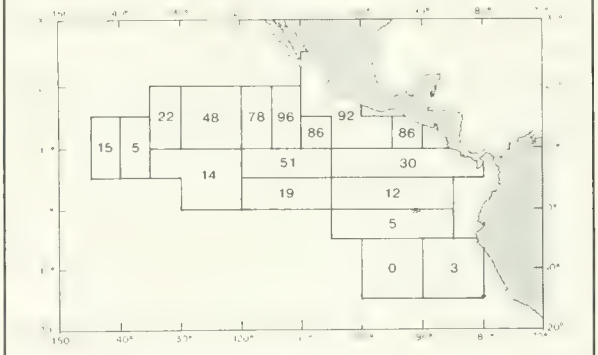

Figure 13
Percentage of adult female spinner dolphins with erect dorsal fins, by area. Of remaining, one had canted fin, others had falcate fins.

cies above 75% in a broad band encompassing the study area south of 15°N (Fig. 9C). Again, *per force*, the steepest gradient was at about 10°N.

Dolphins with intermediate ventral fields (Codes 2–4) were least frequent in the peripheral blocks to the south and southwest and most frequent in a region off Central America below 10°N (Fig. 9B).

Contouring of the ventral-field data based on 5-degree block averages (Fig. 10) yields a clear pattern of extensive, largely Code-1 and Code-5 regions divided by a steep gradient.

Cape

The percentage of dolphins with observed cape was highest in the far south and far west (Fig. 11). This pattern differs from that for the ventral field. For the ventral field (Fig. 9C), the zone of high frequency of Code-5 fields was continuous along a southeast-northwest axis, whereas for the cape the two regions of relatively high frequency in the south and north were separated by a broad zone of relatively low frequency. In addition, the north–south gradient in expression of the cape was not as steep (at 10°N) as for the ventral field.

Dorsal fin

Because of sexual dimorphism and the need to restrict the analyses to sexually mature animals, sample sizes were very much smaller for this character than for the cape and ventral field, necessitating more extensive pooling. Parts of the areas off northern South America and in the southwestern portion of the study area that were included in the coverage for the color pattern characters are not covered in the fin samples.

Despite the reduced resolution in the analyses of dorsal fin variation, some patterns are evident (Figs. 12, 13). In the males the sharp gradient at about 10°N (Figs. 12A, C) is concordant with the pattern for the ventral field (Fig. 9); the canted fin, like the disjunct ventral field, occurred at high frequency (≥75%) only in a region bounded approximately by 10°N and 120°W. The same is true of the erect fin in the female (Fig. 13). The falcate fin in males was more common south of the Equator; 90 of 127 males (71%) in the three southernmost cells that contained no males with canted fins had falcate fins, but only 25 of 66 (44%) in the

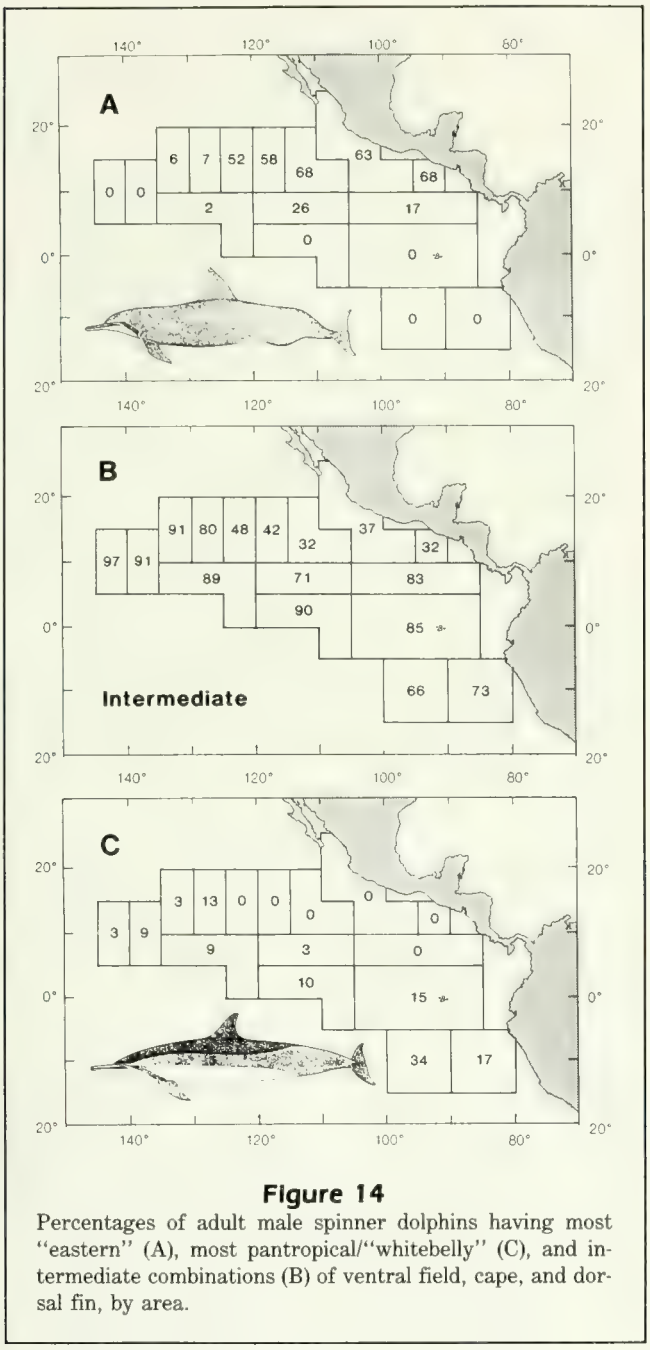

Figure 14

Percentages of adult male spinner dolphins having most "eastern" (A), most pantropical/"whitebelly" (C), and intermediate combinations (B) of ventral field, cape, and dorsal fin, by area.

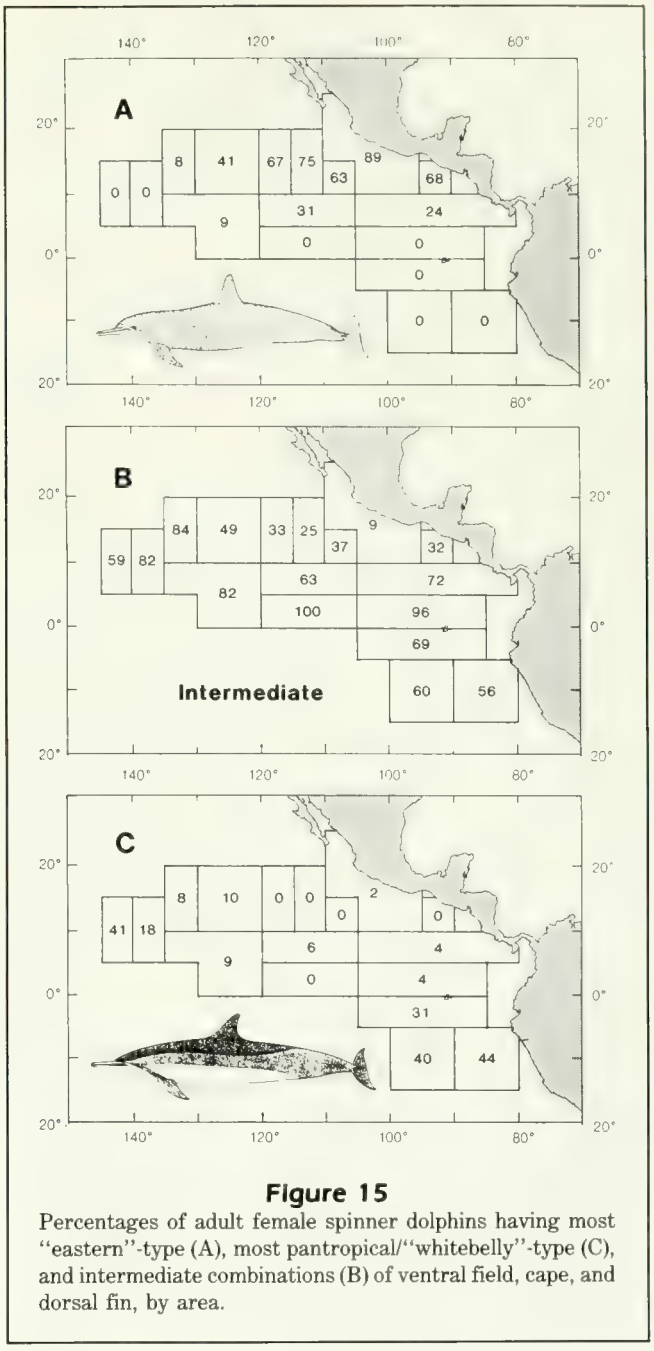

Figure 15

Percentages of adult female spinner dolphins having most "eastern"-type (A), most pantropical/"whitebelly"-type (C), and intermediate combinations (B) of ventral field, cape, and dorsal fin, by area.

two westernmost cells had falcate fins. This difference is statistically significant ($P<0.0001$: Fisher's exact test, two-tailed). The frequency of falcate fins in the two southwestern cells between 10°N and 5°S was intermediate (Fig. 12B). In females, the falcate fin was also most common in the south, although in this case the frequency there was not statistically different from that in the two westernmost cells at $P = 0.05$.

Combined characters

Data on all three characters (ventral field, cape and dorsal fin) were available for 610 sexually adult males and 683 females. The distributions of the extreme expression of eastern character combinations (a total score of 3 for males and 4 for females) and pantropical combinations (10 for both males and females) were similar for males and females (Figs. 14, 15). Only the extreme eastern combination predominated (more than 50%) in any area, in a region bounded by 10°N and

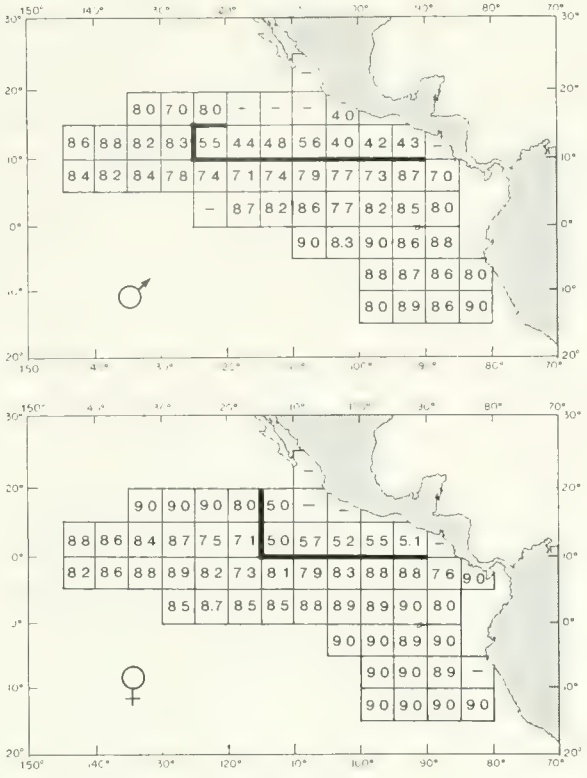

Figure 16

Average combined score for spinner dolphins with intermediate combinations (see Figure 19) of ventral field, cape, and dorsal fin, by 5-degree block (no pooling). Heavy line is between blocks with average score ≥7.0 and those with score <6.

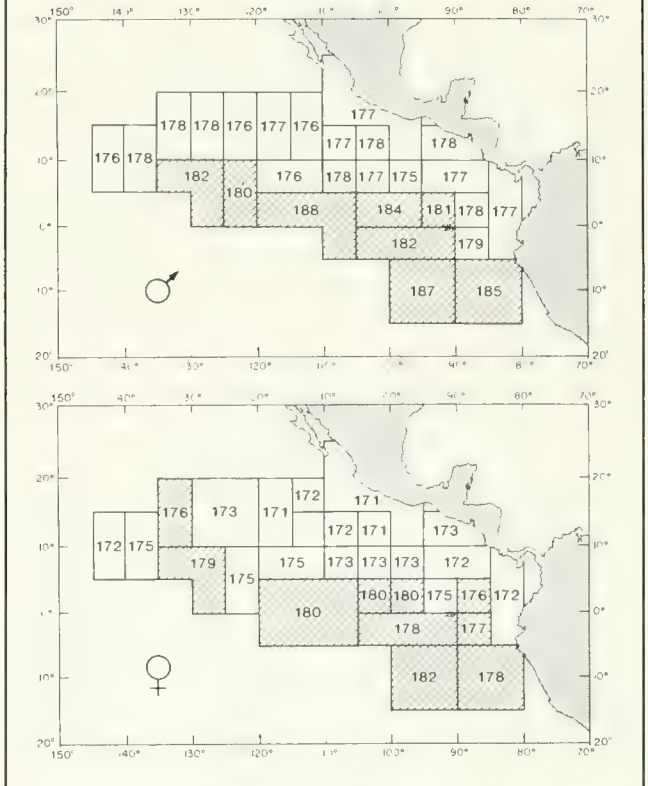

Figure 17

Average body length of adult male and female spinner dolphins, by area. For males, cells with length ≥180 cm are hatched; for females, cells with length ≥176 cm are hatched (adult males are about 4 cm longer than adult females on average; Perrin et al. 1985 and present data).

125°W for males (Fig. 14A) and 10°N and 120°W for females (Fig. 15A). It was absent in the cells south of 5°N and east of 120°W and in the cells west of 135°W. The extreme pantropical combination reached only 34% in males, in the southernmost region (Fig. 14C), and 44% in females (Fig. 15C). It was absent (except for one female) from the cells in which the eastern combination predominated (north of 10°N and east of 120–125°W). It was present only at low levels in the southwestern region, about the same as just to the south and west of the core eastern region. Except in the core eastern region, the majority of dolphins were intermediate (combined scores of 4–9 for males and 5–9 for females (Figs. 14B, 15B); in some cells between 0° and 15°N, over 95% of the adults were intermediate. Even in the core eastern region, about one third were intermediate. The degree of intermediacy was not uniform, however. For both sexes, there was a very steep latitudinal gradient in average scores of intermediate animals at about 10°N (Fig. 16). There was also a steep longitudinal gradient, at about 125°W for males and 115°W for females. Outside this sharply bounded core "eastern" region, variation in intermediate scores was very much less, with only slight N/S and E/W gradients and most animals relatively close to the pantropical extreme.

Proportionately more adult females than adult males in the westernmost cells (west of 140°W) were of the extreme pantropical combination (Fisher's exact test, $P<0.01$), whereas this was not as true in the southernmost cells ($P>0.10$).

Body length

The major shift in average adult length of both males and females (Fig. 17) was at about 5°N, rather than at about 10°N as for the other characters (e.g., compare with Figs. 14–16). The region of smaller animals extended south along the coast of northern South America to about 5°S. Animals from the far west were

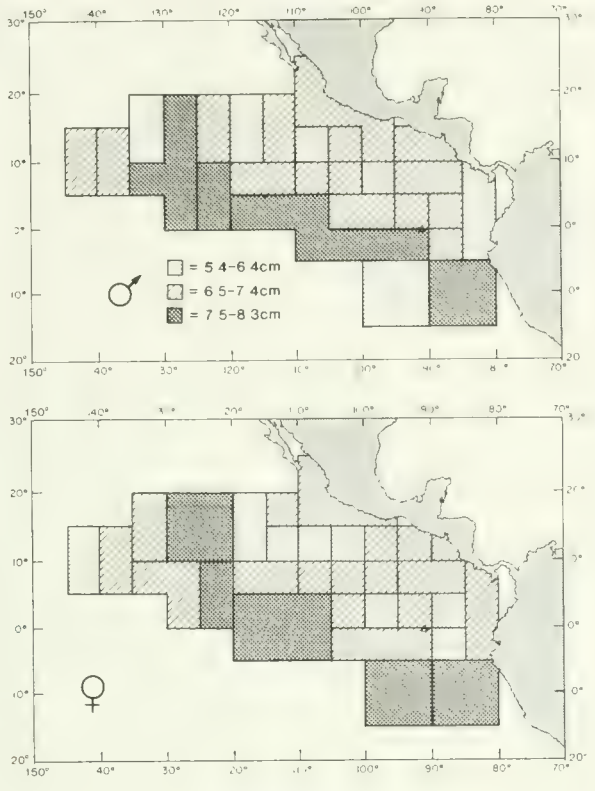

Figure 18
Standard deviations (in cm) of body length for adult male and female spinner dolphins, by area.

more closely associated in average length with those in the east than those in the far south (below 5°S).

Body length is more variable in the regions of greater body length, in both males and females (compare Figures 17 and 18; Table 2).

Table 2
Variability of body length in sexually adult spinner dolphins of eastern (combined scores of 3 for males or 4 for females) and pantropical (combined score of 10 for both males and females) morphology (ventral field, cape, and dorsal fin) from the eastern Pacific.

	Eastern		Pantropical	
	Males	Females	Males	Females
Sample size	136	195	47	78
Average length (cm)	178.9	172.7	181.9	177.2
SD (cm)	6.30	5.90	7.46	7.84
CV	3.52	3.42	4.10	4.43

Discussion

Year-to-year variation and home range

The patterns of distribution of the eastern spinner and the "whitebelly" intergrades/hybrids appear to be relatively stable year to year, although analysis of the present data is complicated by the fact that they come from incidental kills in a very mobile pelagic tuna fishery. The cumulative maps of specimen localities (Figs. 3, 4) show the locations where tuna boats made purse-seine sets that killed spinner dolphins. It reflects only co-occurrence of tuna boats, spinner dolphins, and yellowfin tuna. In addition, the spinner dolphin is not the main target dolphin species in the fishery; the pantropical spotted dolphin *Stenella attenuata* is relatively more often found together with tuna. The sets on spinner dolphins are largely sets on mixed schools of spotted and spinner dolphins; in some areas, especially in the southern and southwestern regions of the study area, spinner dolphins are not often associated with spotted dolphins and seldom are with tuna (Au and Perryman 1985).

Not all regions represented by capture localities in the cumulative maps (Fig. 3) are represented in the maps for individual years (Fig. 4). Possible reasons for this are (1) the dolphins moved around from year to year, (2) the tuna vessels moved around, (3) the yellowfin tuna moved around, and, most likely, (4) some combination of (1), (2), and (3). For some years (e.g., 1985–87), the samples included no spinner dolphins from south of the Equator, but dolphin research survey cruises in that region in 1986 and 1987 made numerous sightings (Holt and Jackson 1987, 1988). That particular hiatus in the maps of localities for at least some years therefore represents the absence of tuna vessels and possibly yellowfin tuna associated with dolphins, not an absence of spinner dolphins. On the other hand, the pattern of paired latitudinal bands of high density of localities for "whitebelly" schools in the cumulative map (Fig. 3) was not apparent in annual plots. It resulted mainly from relatively large numbers of specimens from the area of the upper band in 1975 and 1984–87 and from the lower band in 1977 and 1978. "Eastern" schools were sampled from the region of the northern band in all years. Again, research surveys in 1986 and 1987 sighted comparable numbers of "whitebelly" spinner schools in the two regions. In this case, it is possible that the pattern or degree of association of tuna with the two forms varied interannually. However, the numbers of sightings of spinner dolphins during all the research cruises were relatively small, and it remains possible that some portion of the patterning in the cumulative distribution represents inter-

annual variation in distribution; i.e., the northern boundary of the main "whitebelly" distribution may fluctuate year to year by about 5 degrees of latitude. This would be consistent with some of the results of the present study; for example, the intermediate percentages of the extreme "eastern" and "whitebelly" character states in the band between 5° and 10°N (Figs. 9–10, 12–15).

Another possible explanation of the latitudinal pattern has to do with distribution of tuna-fishing effort. During the period 1976–79, the Inter-American Tropical Tuna Commission set a regulatory demarcation line at 5°N, between 95° and 110°W. During this period, when an annual areal quota of yellowfin tuna for the region north of the line was filled, the international fleet was forced to fish south of the line or to the west (Peterson and Bayliff 1985). A similar line was in force in 1973–75 at 3°N. The subsidiary latitudinal band of distribution records south of 5°N apparent in the spinner dolphin data is also present in data for the pantropical spotted dolphin *S. attenuata*, the principal target species of the tuna fishery (Perrin et al. 1983). Illustrations of the effect of the regulatory regime on the distribution of fishing effort are given in Punsley (1983); the effect was particularly pronounced in 1978.

Some of the morphological results speak against the hypothesis of large-scale latitudinal movements. Variation among sub-areas of the "whitebelly" range is discordant. For example, for the character "ventral field" (Figs. 9, 10), the far-western blocks, far-southern blocks, and southwestern blocks are similar in having relatively high frequencies of the Code-5 character state (most "whitebelly-like"), while for the "cape" (Fig. 11), the southwestern region differed from the west and south in having low frequencies of observed cape (they were most like the animals immediately to the north). For male/female dorsal fin shape (Figs. 12, 13), the southern blocks had higher frequencies of the falcate fin than did the western blocks. While in color pattern and in cranial characters (Schnell et al. 1985), the westernmost blocks were most like the southern blocks, in body length and variability of body length (Figs. 17, 18) they were most like the northern and central blocks. The blocks just north of the Equator were remarkable in having very high frequencies of females intermediate between the most "whitebelly" state and the most "eastern" state in combined character scores (Fig. 15); the highest frequencies of these in males were in the westernmost blocks. In body length in both males and females (Fig. 17), the steepest gradient was at about 5°N, whereas in combined ventral field, cape and dorsal fin (Figs. 14, 15), it was at about 10°N. In cape (Fig. 11) and body length (Fig. 17), the dolphins in the Panama Bight and just to the south were most like those in the core "eastern" region (lacking visible cape and small in body size), but in ventral field (Fig. 9) they were intermediate between those to the north and south, having approximately equal frequencies of Code 1, Code 5, and summed Codes 2–4. This complex patchwork of variation suggests that there is not a large amount of movement between the various regions and that the year-to-year variation in the collection localities (Figs. 3, 4) reflects mainly movements of the tuna vessels and perhaps the tuna.

The complex geographical pattern of variation in the zone of intergradation/hybridization ("whitebelly spinners") is consistent with the limited information from tag returns (Perrin et al. 1979b), which suggests a home range of a diameter of hundreds rather than thousands of kilometers. This is also supported by the stability of the core eastern region between years and patterns of reproductive seasonality that suggest areal structure within the eastern region (Barlow 1984).

However, there may be mid-scale seasonal movements within an overall pattern of interannual stability, especially in the "whitebelly" areas outside the core range of the eastern spinner. Based on census surveys from dedicated research vessels, Reilly (1990) reported increases in abundance west of 120°W along 10°N coincident with seasonal shoaling of a thermocline ridge. Because of interannual variation in distribution of tuna fishing effort (discussed above), the coarse geographic strata used, and the relatively small sample sizes for the outlying strata, the present analyses probably could not be expected to detect such shifts, although the shifts might be expected to blur the perceived patterns of morphological gradients.

Taxonomic status and management of the "whitebelly" spinner dolphin

The "whitebelly" spinner has been managed as two "stocks" divided at the Equator, the northern whitebelly spinner and the southern whitebelly spinner, implying effective reproductive isolation between them and from the eastern spinner (e.g., Hall and Boyer 1990). The complex pattern of discordant geographic variation and the relatively higher standard deviations (of body length) in the range of the "whitebelly" spinner are typical of a hybrid zone resulting from what Mayr (1970) called allopatric hybridization, or "the formation of a secondary zone of contact and of partial interbreeding between two formerly isolated populations that had failed to acquire complete reproduction isolation during the preceding period of geographic isolation." The discordant pattern speaks against the earlier hypothesis of a locally adapted "whitebelly" population sharing features with populations to the east and west and defined by morphological clines. An

hypothesis of secondary contact after isolation (Perrin et al. 1985) and consideration of the patterns of variation led to the formal recognition of the eastern form as a subspecies, *Stenella longirostris orientalis*, and the "whitebelly" form as an hybrid/intergrade between that subspecies and the pantropical spinner dolphin *S. l. longirostris* (Perrin 1990). The hypothesis of genetic exchange between the eastern and "whitebelly" populations is also supported by results of analysis of mitochondrial DNA (Dizon et al. 1991); the presence of unique haplotypes that would be expected in isolated populations was not detected. Given this situation, a relatively higher priority should probably be given to protection of the eastern subspecies on the grounds that it is a distinctly and locally adapted form vulnerable to depletion and to genetic "swamping" from the larger and less-exploited population to the west. In any case, the understanding presented here of the complex pattern of variation within the "whitebelly" range does not support the present division into northern and southern stocks for management on grounds of population distinctness.

Conservation and management of the eastern spinner dolphin

There was generally good concordance between the patterns in the individual morphological characters and the relative distributions of the two kinds of schools as identified by modal appearance (Fig. 3). One exception was the region west of the Bight of Panama; here the very high frequency of morphologically intermediate dolphins and virtual absence of animals of the extreme "eastern" appearance indicate that these schools perhaps would have better been identified as "whitebelly" schools. Apart from this discrepancy, the concordance between the character patterns and the field identification of schools suggests that the modal-appearance method of identification is largely effective. The substantial number of "mixed schools" and unidentified schools, however, indicates that the method can still offer difficulties. In addition, it is sometimes difficult to identify a school of spinner dolphins to "stock" (eastern or "whitebelly") before the seine is set. This can be due to poor viewing conditions (time of day, angle of sun, amount of wind, height of swell) or to the behavior of the dolphins (e.g., "laying low," precluding observation of ventral coloration).

An alternative management scheme based on geographic location would avoid the difficulties of field identification of schools. Although the working hypothesis for management of the eastern spinner and the "whitebelly" spinner (eastern/pantropical hybrids or intergrades) has been one of broadly overlapping ranges (e.g., Perrin et al. 1985), the actual transition between the two as indicated by gradients in the morphological characters and the field identifications (Fig. 3) is quite sharp. An "eastern spinner conservation zone" could be devised that would offer appropriate and unequivocal protection to the unique and coherent gene pool of the eastern subspecies. For example, such a zone bounded by 10°N latitude and 125°W longitude, the approximate latitude and longitude of the major gradients in the morphological characters, would have included 84% of the schools identified in the field as "eastern" (excluding those in the Bight of Panama, discussed above) and only about 5% of those identified as "whitebelly" (Fig. 19). Implementation of an international quota or prohibition for such a zone would be straightforward. The boundaries could be set based on a balance of considerations of conservation and operational practicality and should take into account seasonal and interannual variation in locations of concentrations of schools of the eastern spinner.

This scheme, of course, is only one of numerous possible alternatives to conservation and management of

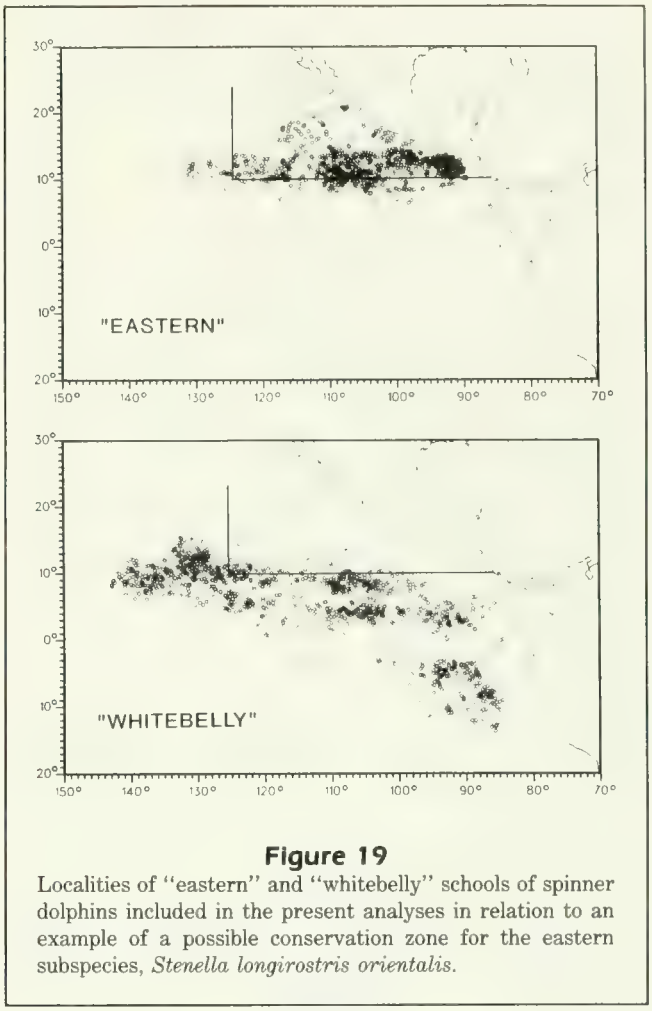

Figure 19
Localities of "eastern" and "whitebelly" schools of spinner dolphins included in the present analyses in relation to an example of a possible conservation zone for the eastern subspecies, *Stenella longirostris orientalis*.

the subspecies. Others include international application of a stock quota, complete bans on this type of fishing, and increased focus on technological efforts to reduce fishing mortality rates, to name a few.

The Central American spinner ("Costa Rican spinner")

The number of "Costa Rican" schools sampled was too small for meaningful separate analysis (2 of 1454; Fig. 3) and the effect on the analyses of including them in the pooled samples can be considered negligible. In any case, the range of the Central American spinner *S. l. centroamericana* as presently understood (a coastal strip about 50nmi wide between about 13° and 7°N) does not overlap those of the eastern subspecies or the "whitebelly" hybrid/intergrade forms (Perrin 1990). This range could serve as a management unit for the subspecies.

Acknowledgments

The data used in this study were collected by biological technicians aboard commercial tuna seiners. We wish to thank these people and the captains and crews of the seiners; the research would have been impossible without their efforts and support. The sampling programs were supported by the U.S. National Marine Fisheries Service and the Inter-American Tropical Tuna Commission; both agencies gave us full access to data and specimens. R.B. Miller and others processed reproductive samples to determine sexual maturity. K.E. Wallace and R. Rassmussen provided data extraction services. R.C. Holland gave invaluable assistance with the contouring. J. Barlow carried out the Fisher's exact tests. R.M. Allen drafted the figures. J. Barlow, M. Scott, A.E. Dizon, I. Barrett, and S.B. Reilly reviewed the manuscript and offered many useful suggestions.

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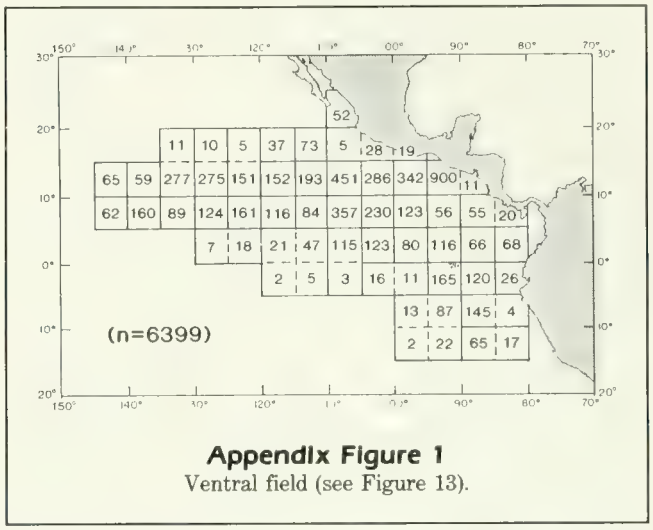
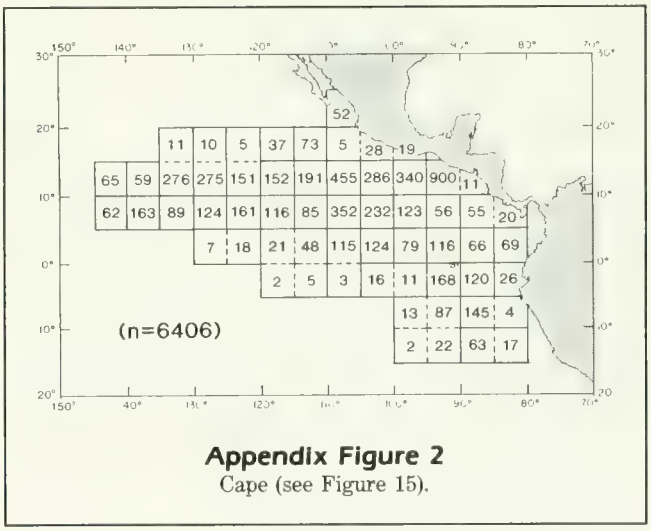
Appendix

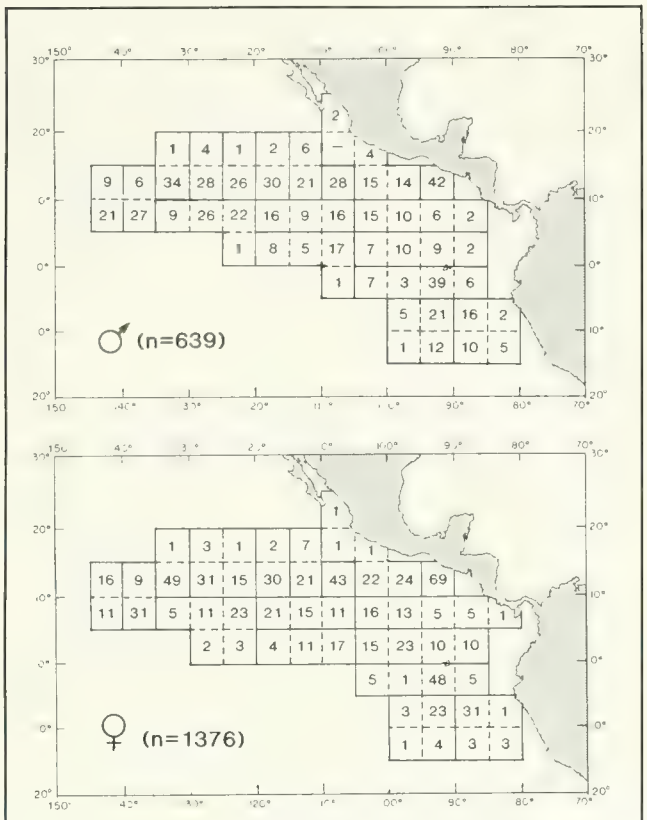
Sample sizes by 5-degree block and pooling for analyses of geographical variation in external morphology of the spinner dolphin (blocks separated by dashed lines were pooled).



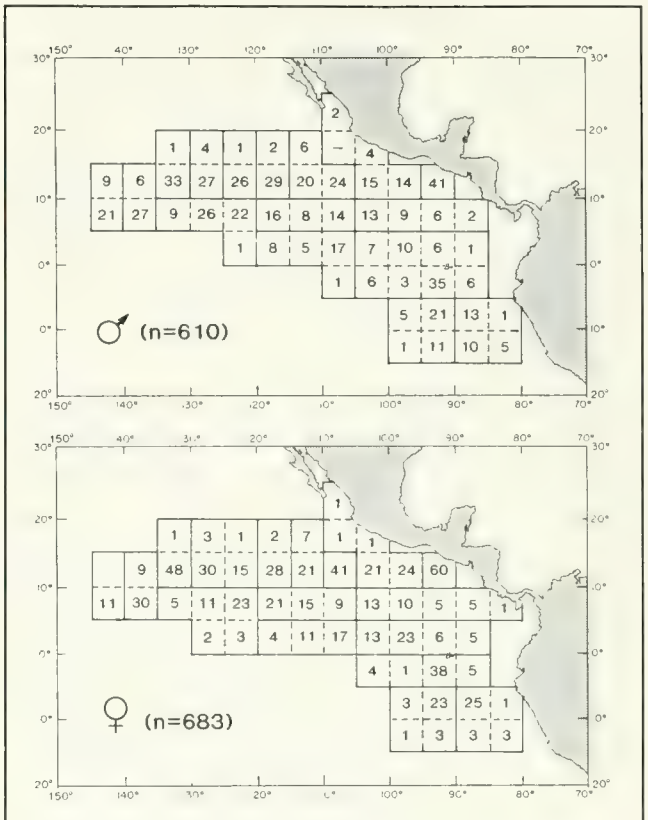
Appendix Figure 1
Ventral field (see Figure 13).



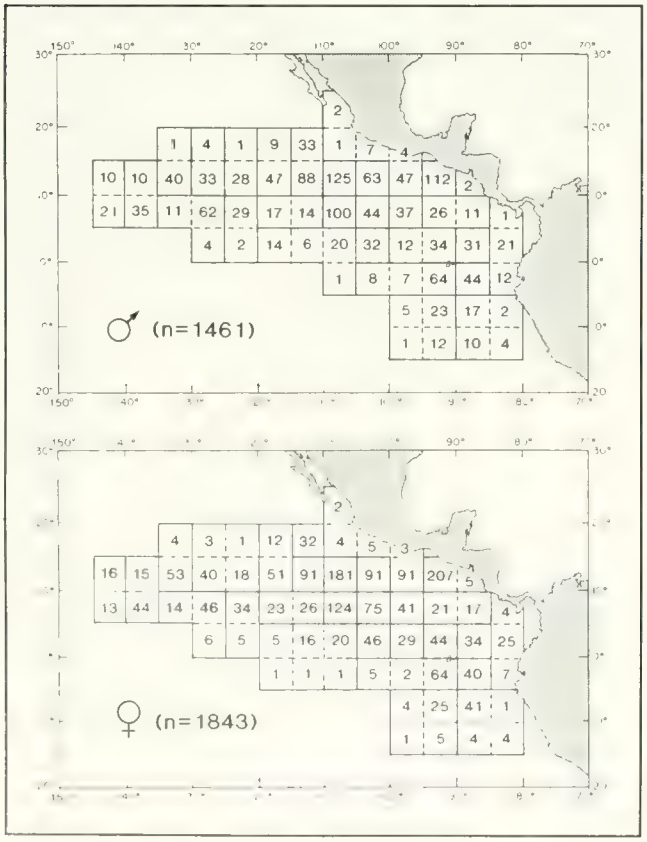
Appendix Figure 2
Cape (see Figure 15).



Appendix Figure 3
Dorsal fin (see Figures 15 and 17).



Appendix Figure 4
Combined scores for ventral field, cape and dorsal fin (see Figures 18 and 19).



Appendix Figure 5
Body length (see Figures 21 and 22).

Satellite observed Sea-surface Temperatures and Yellowfin Tuna Catch and Effort in the Gulf of Mexico

James H. Power

Coastal Fisheries Institute, Center for Wetland Resources
Louisiana State University, Baton Rouge, Louisiana 70803

L. Nelson May Jr.

Coastal Fisheries Institute, Center for Wetland Resources
Louisiana State University, Baton Rouge, Louisiana 70803
Present address: Southeast Fisheries Center, National Marine Fisheries Service, NOAA
Bldg. 1103, Room 218, John C. Stennis Space Center
Stennis Space Center, Mississippi 39529

Abstract.– A substantial longline fishery has recently developed in the Gulf of Mexico. Tuna are believed to aggregate in regions of sea-surface temperature change (frontal zones), and this behavior may significantly bias the catch and effort statistics critical for managing the fishery. We report the results of an effort to relate the sea-surface thermal structure evident in satellite imagery to yellowfin tuna *Thunnus albacares* catch and effort, with the goal of providing fishery managers an assessment of how the yellowfin tuna catch-per-unit-of-effort (CPUE) is affected by the presence/absence of temperature variability. We examined over 6000 longline set records and 109 satellite sea-surface temperature (SST) images, and compared the CPUE with sea-surface temperature statistics computed from image data in the corresponding area of the longline set. We found no discernable relationship between image SST statistics and CPUE, and conclude that catch statistics in the northwestern Gulf of Mexico are not biased by yellowfin tuna aggregating in regions of SST variability.

Manuscript accepted 25 February 1991.
Fishery Bulletin, U.S. 89:429–439 (1991).

Satellite sensors that detect ocean color or temperature have repeatedly confirmed that the ocean environment is highly structured, with the juxtaposition of different water masses forming frontal zones where important parameters such as salinity, temperature, and nutrient concentration can change rapidly over short horizontal distances. In turn, phytoplankton, zooplankton, and nekton abundances may also change significantly in these regions, either in response to favorable nutrient/food conditions or by accumulating in converging currents. Because the surface water mass boundaries are sometimes discernable in satellite imagery, the locations of associated phytoplankton, zooplankton, and pelagic fish assemblages can sometimes be determined from such imagery (Thomas and Emery 1988, Klimley and Butler 1988).

Large and commercially important pelagic fishes, such as tuna, are thought to respond to increased food concentrations or other favorable conditions by aggregating in these frontal regions (Alverson 1961, Beardsley 1969, Laurs et al. 1984, Maul et al. 1984, Fiedler and Bernard 1987, Klimley and Butler 1988). Fishermen have long believed that fishing near thermal or color fronts would increase fishing success, and sometimes refer to presumably favorable waters as "tuna water" (Alverson 1961). The fisherman's ability to locate such frontal zones is usually limited by the field of coverage available from his vessels for sampling temperature (or color) or that of a spotter pilot's ability to detect color boundaries. Because satellite sensors can now detect ocean temperature or color over large geographic areas, pilot projects to use satellite imagery as a fisheries aid have been undertaken on both the east and west U.S. coasts (Breaker 1981, Montgomery 1981, Wittenberg-Fay 1986, Cornillon 1986).

Efforts to provide sea-surface temperature (SST) charts as fisheries aids have been accompanied by scientific investigations to evaluate the possible relationships between SST, ocean color, and fishing success. Laurs et al. (1984) used thermal and ocean color imagery from the Coastal Zone Color Scanner to relate albacore *Thunnus alalunga* catch to oceanographic features in the eastern Pacific, and concluded that albacore catch was clearly associated with

oceanic color and thermal fronts apparent in the imagery. They also observed that shoreward intrusions of oceanic water were coincident with notable albacore aggregations. Laurs et al. (1984) based their conclusions on a visual analysis of catch rates superimposed on images, and did not present any statistical analyses, such as relating catches to distances from frontal regions. Fiedler and Bernard (1987) analyzed satellite imagery and stomach contents data taken from albacore and skipjack *Katsuwonus pelamis* and demonstrated that these fish were opportunistically feeding on prey items associated with frontal regions off the California coast.

Maul et al. (1984) utilized satellite imagery to compare SST with Atlantic bluefin tuna *Thunnus thynnus thynnus* catches reported by the Japanese longline fishery that operated in the Gulf of Mexico during 1979 and 1980. The 1980 catch was substantially higher than that of 1979, and Maul et al. (1984) attributed the increased catch to the shift of fishing activities closer to the frontal zone associated with the Loop Current edge. They stated that 85% of the 1980 catch was taken within 100 km of the Loop Current. In contrast to the Laurs et al. (1984) study, much of the Maul et al. (1984) analyses were quantitative, rather than qualitative, since the distances from the locations of bluefin catches to the edge of the Loop Current were analyzed.

Herron et al. (1989) continued efforts to quantify the relationship between fish catches and temperature structures in the Gulf of Mexico by analyzing 20 sea-surface temperature (SST) images acquired concurrently with trawl catches of the demersal butterfish *Peprilus burti*. They calculated statistically significant regressions relating butterfish trawl catches to SST gradients computed from satellite imagery.

In their study of tuna catch in the Gulf of Mexico, Maul et al. (1984) concentrated on bluefin catches relative to the edge of the Loop Current. In addition to the Loop front, there are numerous other coastal and oceanic regions of rapid temperature change that are potentially important aggregators of tuna. For example, Huh et al. (1978) described extensive coastal and shelf thermal patterns in the northeastern Gulf of Mexico that were present during 1976–77. Although extensive cloud cover and regions of near-isothermal SST values occur in the Gulf of Mexico during the summer months (Huh et al. 1978), considerable variation in SST is evident in satellite imagery collected during the fall through spring months. Figure 1 is an image of Gulf of Mexico SST patterns on 21 March 1988, and demonstrates the intricate thermal patterns that can be present in the northern Gulf of Mexico.

A U.S.-based fishery for bluefin and yellowfin tuna *Thunnus albacares* has rapidly developed in the Gulf of Mexico. Although Japanese longline vessels harvested considerable numbers of yellowfin tuna during 1963–81 (Wilson 1988), domestic landings prior to 1983 were relatively low and primarily the result of bycatch from swordfish *Xiphias gladius* fishermen. By 1986, however, Louisiana landings had leaped to 24 million pounds (Adams 1987). In the same year, 3.4 million pounds of yellowfin tuna were landed in the west coast of Florida, with the majority landed in the panhandle region. These fishermen frequently rely on ocean-surface temperature to judge where to set their lines. The conventional wisdom is to set lines when a temperature change of a "couple degrees" is detected.

At the present state of knowledge, assessment and management of the tuna resource must depend on catch statistics to indicate changes in overall stock size. Catch-per-unit-of-effort (CPUE) can be elevated if fishermen locate tuna that may have aggregated at fronts or regions of rapid temperature change; alternatively, the CPUE may be depressed by the absence of fronts or the fisherman's inability to locate them. In either case, the data used for assessment and management decisions could be biased to an unknown extent by the possible concentrating effect of frontal boundaries. This research was intended to explore possible relationships between the Gulf of Mexico SST structure observable in satellite imagery and the yellowfin tuna catch and effort, and to determine whether regions of temperature change yield increased fishing success.

Methods

There were three primary components to the research: (1) Acquisition, validation and summarization of the seasonal and spatial patterns in the longline fishery catch and effort data; (2) development of a satellite image database and description of the seasonal and spatial patterns in SST; and (3) investigation of any associations between the two data sets.

Data on longline sets were acquired from longline logbook records compiled by the National Marine Fisheries Service (NMFS). Data were from domestic fishery longline sets in the Gulf of Mexico and western Atlantic spanning September 1986–December 1987. These records included date, location of set, length of longline in miles, number of hooks fished, and number of fish caught. Catch records without valid latitude and longitude coordinates were deleted, as were records outside the Gulf of Mexico (east of 80°30′W longitude and south of 6°N latitude). Data such as time of day and duration of set, bait used, sizes of fish caught, or whether the reported geographic coordinates represented the location of the beginning or end of the set, were not available for our analyses. The total number

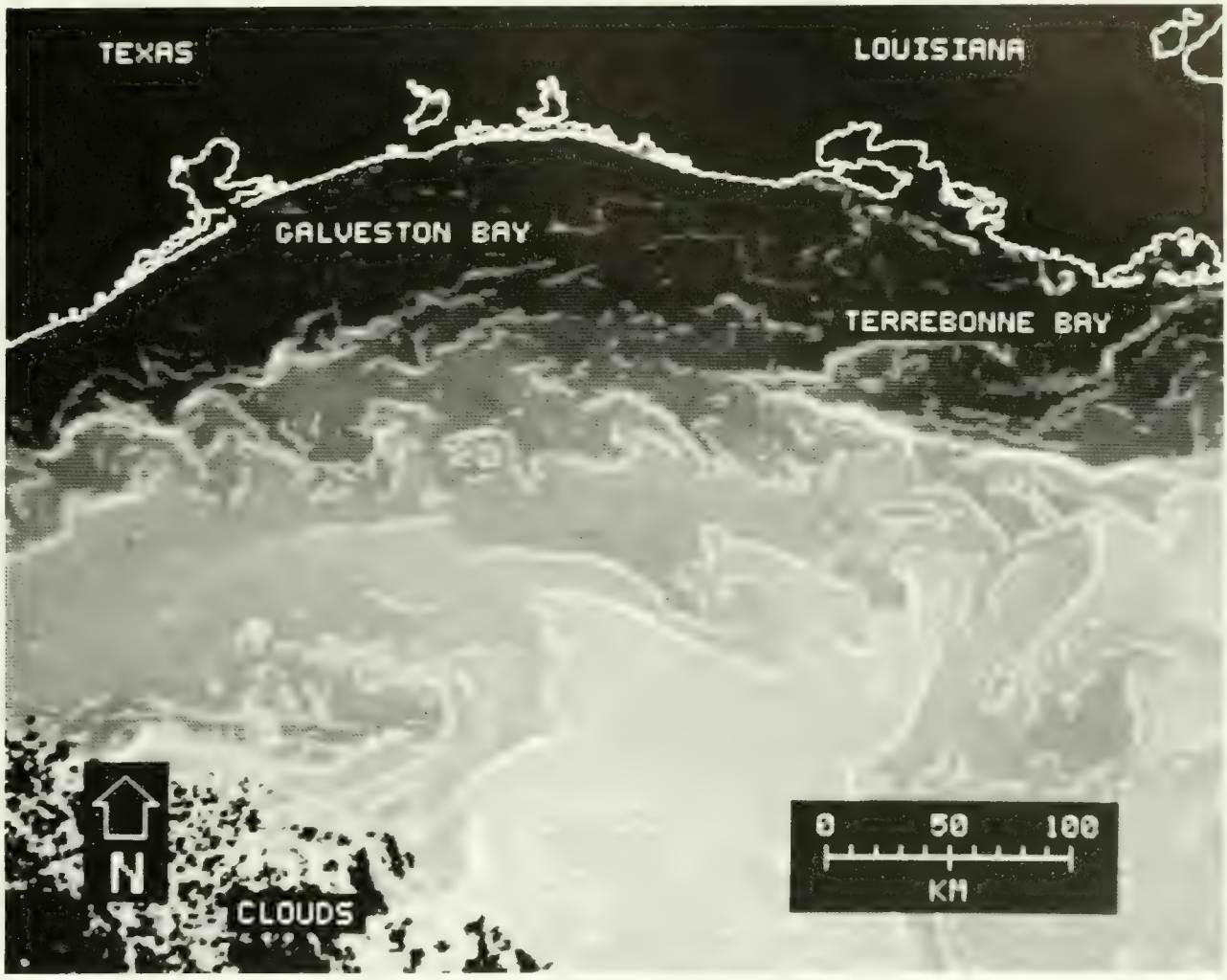


Figure 1
Enhanced satellite sea-surface temperature image of the northern Gulf of Mexico acquired by the NOAA-9 satellite on 21 March 1988.

of sets available for analysis was 6618. The median longline length deployed was 24 miles, although some sets were recorded as over 70 miles long. The median number of hooks per set was 576, and the median number of hooks per mile of set was 24. Yellowfin tuna CPUE was computed by combining the number of fish kept with the number discarded, and tabulating CPUE as the total number of fish caught per 1000 hooks per set.

The satellite image database was developed from a total of 109 Advanced Very High Resolution Radiometer (AVHRR) images of the Gulf of Mexico obtained from archives maintained by the National Environmental Satellite Data Information Service (NESDIS) and NMFS. The imagery was acquired by the NOAA-9 and NOAA-10 satellites. In selecting images for analysis, an effort was made to exclude those containing significant cloud cover. This selection was made either by NMFS personnel while compiling their image archive, or by us during examination of images in the NESDIS archives. Although a total of ten images acquired during August–September 1987 were obtained from NMFS and included in the analysis, we did not obtain additional summertime imagery for the study, since SST in the Gulf is nearly isothermal during that time of year (Huh et al. 1978; see also summer month editions of the Oceanographic Monthly Summary). Consequently, the image database, and subsequent statistics, are biased with respect to the summer months and periods when significant cloud cover was present in the Gulf.

The National Oceanic and Atmospheric Administration (NOAA) satellites record image data in four or five bands: two in the reflected solar region of the spectrum and two or three in the emitted thermal region. The spatial resolution of the sensors is 1.1 km at nadir, increasing to about 5.5 km at the edges of the 2580 km-wide scan. The AVHRR data were processed into sea-surface temperature (SST) images using a TeraScan* computer system operated by the School of GeoSciences at Louisiana State University. The TeraScan system consists of a computer, color image display device, and other custom hardware and software designed to process AVHRR digital imagery. The images were digitally cut to fit a master image that encompassed the entire Gulf of Mexico (latitude 17°45.30′N to 30°44.70′N and longitude 81°0.33′W to 97°59.67′W).

Daytime images were calibrated and converted to SST using the multichannel SST algorithm (MCSST) described by McClain et al. (1985). Radiometric noise in channel 3 caused some difficulties in deriving SST from nighttime images. Spatial filtering techniques (Schowengerdt 1983) performed on the channel 3 image prior to computing the SST had little or no effect on the noise and often resulted in significant degradation of the information content in the completed image. Although image restoration techniques such as filtering in the frequency domain appear to have been successful in minimizing noise in channel 3 (Warren 1989), they were not a practical consideration for this project because of the large number of images to be processed and computer software limitations. Thus, channel 3 data were removed from each nighttime image file prior to processing data into SST. Since the nighttime processing technique was an untested modification of the MCSST algorithm, a linear regression analysis was used to compare the satellite-derived SST data with *in situ* Gulf of Mexico SST data obtained from NOAA weather buoys. Residuals were plotted by the date and time of image acquisition, satellite number, and buoy locations to look for potential bias in SST values that may have been related to the processing technique.

Since atmospheric effects can significantly reduce the reliability of satellite-derived SST measurements, particularly as the viewing angle increases from nadir, a threshold was defined to identify image data acquired at a satellite zenith angle of greater than 53 degrees. These pixels were digitally masked and therefore excluded from further processing.

The SST images were coregistered to an equidistant cylindrical projection (Snyder 1987) using least-squares transformation equations and the nearest-neighbor resampling technique (Lillesand and Kiefer 1979). They were then reformatted for additional processing with version 8.0 of the Science and Technology Laboratory Applications Software (ELAS) (Beverly and Penton 1989). ELAS was installed on a MicroVAX 3600 computer and a MicroVAX 3500 workstation and provided advanced spatial processing utilities required during the second phase of the analysis. A processing protocol was developed using sequential ELAS commands and VAX software utilities to analyze the SST images and transfer selected data and tabulations to the Statistical Analysis System** for statistical analysis and plotting. A binary mask constructed from the World Data Bank II digital coastline file (Gorney 1977a, b) was used in each processing stream to exclude land pixels from the analyses. This protocol was used for all subsequent processing during the study. The initial analysis of each SST image consisted of Gulf-wide tabulations of temperature frequencies and cloud pixels.

The magnitude of surface temperature gradients (MSTG) was derived from each SST image using Sobel operators and simple image arithmetic (Gonzales and Wintz 1977). Sobel operators use the 3×3 moving window technique to extract vertical (north-south) and horizontal (east-west) temperature gradients from digital images. The MSTG was computed by summing the absolute value of the horizontal and vertical gradient information (Gonzales and Wintz 1977). The result of this operation is that each pixel location is assigned a numerical value that indicates how greatly SST at that location differs from that of surrounding pixels. This gradient value is independent of the direction of temperature change. An additional masking operation was performed on each MSTG image to exclude contaminated pixels adjacent to the land and cloud masks that were created as an artifact of the moving window technique.

The possible relationships among thermal features and yellowfin tuna CPUE was examined by computing summary statistics (e.g., mean, median, coefficient of variation) of the SST and MSTG data for circular regions of sea surface encompassing each longline set. Since the orientation and initial and final geographic coordinates of the sets were not available, we defined three concentric circular areas encompassing each reported location of a longline set. The recorded location of the set was the center of these circular areas, while the radii were specified as the length of the longline set, one-half the length of the set, and one-

*TeraScan is a proprietary computer system marketed by SeaSpace, 3655 Nobel Drive, Suite 160, San Diego, CA 92122.

**The Statistical Analysis System is a proprietary computer software package marketed by the SAS Institute, Box 8000, Cary North Carolina 27511-8000.

quarter the length of the set. We assumed that these circular sampling areas represented the area fished by the gear and/or traversed by the fish during the set. The mean, median, and coefficient of variation of the SST and MSTG pixel values contained within the three concentric circular regions were computed for each set. These SST and MSTG statistics computed for the circular regions (polygons) encompassing the sets were then plotted against the corresponding yellowfin tuna CPUE at that same location. The potential bias due to spatial and temporal variation in cloud coverage was examined by classifying each circular polygon into one of three groups based on the percentage of cloud cover (25–49%, 50–74%, >74%) and comparing the results with CPUE and the statistics tabulated from the image data. Plots of CPUE versus the circular polygon statistics by month were also done to determine whether associations between SST variability and yellowfin tuna CPUE were present only at certain times of the year.

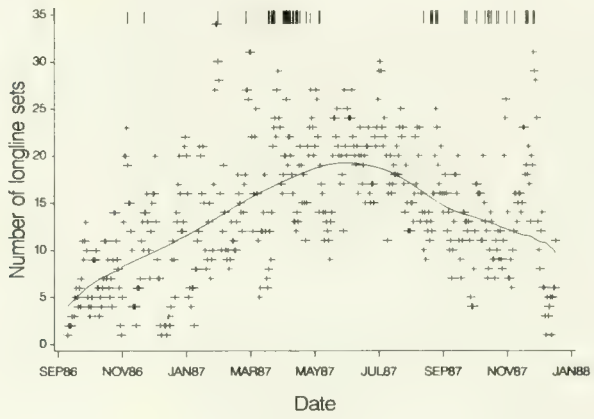


Figure 2

Number of longline sets reported each day in the Gulf of Mexico, September 1986–December 1987. Curve is fit using robust locally-weighted regression (Cleveland 1979). Vertical bars at the top margin of the plot are drawn at the corresponding dates of the satellite images used in the analyses.

Results

Yellowfin tuna database

The fishery data include only records for which geographic coordinates were available. In that respect, the results may be biased if longline sets records lacking geographic coordinates occurred in a given region, or had anomalously high or low yellowfin tuna catches.

The longline fishery operated nearly every day in the Gulf of Mexico from September 1986 to December 1987. Usually 10–20 sets were recorded each day, with very few days when no sets were reported (Fig. 2). The frequency of sets appeared to increase in late 1986 to midsummer 1987, followed by a decline in autumn (Figure 2 and subsequent figures include a curve, similar to a running mean, that was fit using Cleveland's (1979) technique of robust locally-weighted regression). Fishing effort during 1986–87 was heavily concentrated in the northwestern Gulf of Mexico, where extensive seasonal variation in SST was observed. Sets were mainly deployed between 26°N and 29°N latitude, and were fairly uniformly distributed west of the Mississippi River Delta between 88° and 96°W longitude (cf. Fig. 3).

Yellowfin tuna are apparently present and available to the longline fishery, at least in small numbers, throughout the year, since 79.2% of the sets caught one or more yellowfin tuna (Fig. 4). There was a noticeable decline in the daily percentage of sets catching at least one yellowfin tuna in the early months of 1987 (Fig. 4), but because the data set did not cover

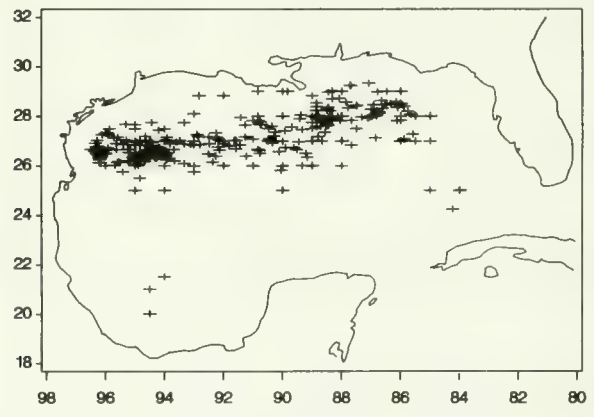


Figure 3

Geographic location of longline sets deployed in the Gulf of Mexico during March 1987.

multiple years, it is uncertain whether this is an annual phenomenon.

The mean yellowfin CPUE for the entire data set (6618 sets) was 14.2 fish/1000 hooks with a standard deviation of 18.9. The median CPUE was 8.9 fish/1000 hooks. These CPUE figures are comparable to those reported by Polacheck (1989) for yellowfin tuna in the Pacific. The daily mean yellowfin CPUE may be elevated in the fall months and depressed during the late-winter and early-spring months (Fig. 5).

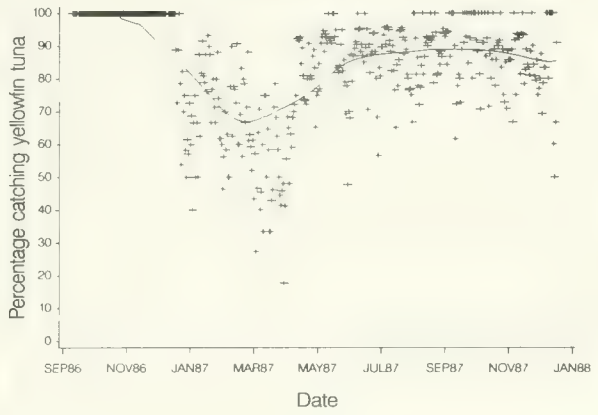


Figure 4

Daily percentage of longline sets that caught one or more yellowfin tuna in the Gulf of Mexico. Curve is fit using robust locally-weighted regression.

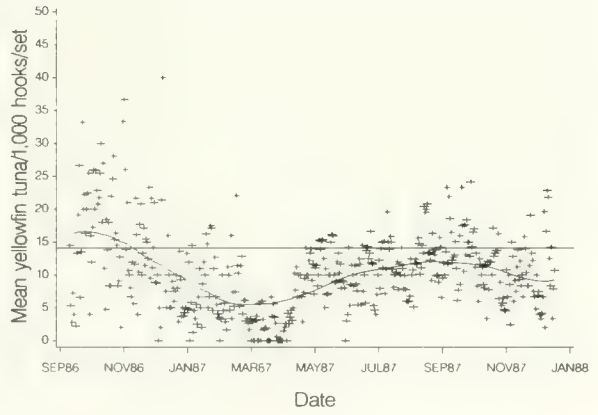


Figure 5

Daily mean yellowfin catch/1000 hooks in the Gulf of Mexico, 1986–87. Straight line is overall mean yellowfin CPUE. Curve is fit using robust locally-weighted regression.

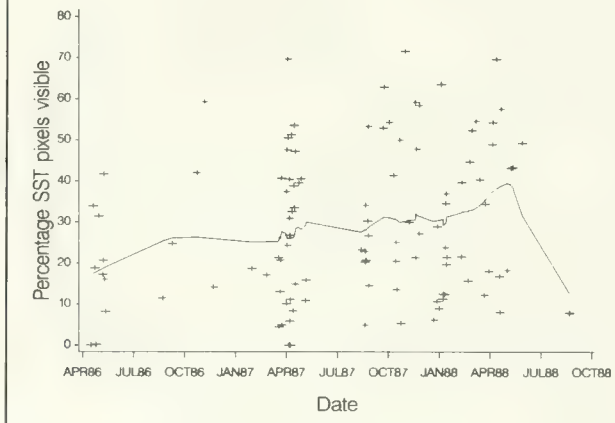


Figure 6

Percentage of cloud-free water pixels used to derive sea-surface temperatures from Advanced Very High Resolution Radiometer satellite images used in the study, 1986–88. Curve is fit using robust locally-weighted regression.

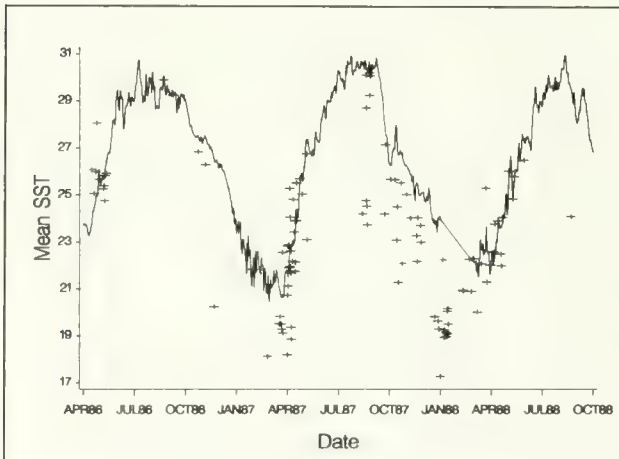


Figure 7

Mean satellite-derived sea-surface temperature (SST) for the Gulf of Mexico derived from Advanced Very High Resolution Radiometer imagery, 1986–88. Curve is daily mean surface temperature recorded at National Weather Service data buoy 42001, located at latitude 25.9°N, longitude 89°W.

Image database

The regression analysis of satellite-derived SST with the buoy SST data showed acceptable agreement between the two temperature values (r^2 0.902, n 206; Fig. 7). There was some tendency for SST from satellites to be lower than those from buoys at the higher temperature ranges, with the imagery acquired by NOAA-10 satellite accounting for most of the variation.

The geographic region in this study, excluding land, covered 1,512,272 ocean surface pixels. Cloud cover and/or the position of the satellite track reduced the number of pixels available for analysis in each image. Image coverage of the study region ranged from less than 1% to 70% of the available pixels, with no seasonal pattern to the coverage (recall that summertime images were generally excluded from the analyses) (Fig. 6). Figures 6 and 7 also portray the temporal coverage of the imagery used in our analyses. The mean image-wide derived SST and the daily mean surface temperature recorded at the National Weather Service data buoy 42001 (latitude 25.9°N, longitude 89°W) both follow

the expected seasonal progression of SST (Fig. 7). Of note is the more rapid warming of SST in spring of 1987 compared with the spring of 1988. The SST coefficient of variation can be viewed as a broad index of how "structured" the sea-surface temperature is (Fig. 8). There was a clear seasonal trend to this statistic during 1986–87, indicating that considerable spatial variation in SST was present from the winter through early spring. The warming of SST during the spring months to more isothermal conditions, mentioned previously, is coincident with a decline in the SST coefficient of variation.

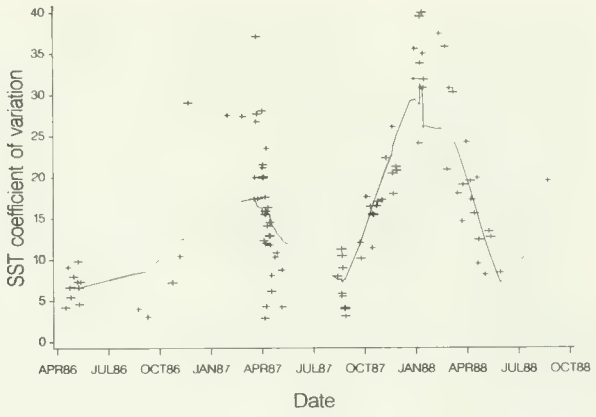


Figure 8

Coefficient of variation of sea-surface temperature (SST) for the entire Gulf of Mexico derived from Advanced Very High Resolution Radiometer imagery, 1986–88. Curve is fit using robust locally-weighted regression.

Image and yellowfin tuna CPUE relationships

Regions of rapid sea-surface temperature change appear as lighter lines in the gradient image (Fig. 9). Superimposed on this image are the locations of longline sets (crosses), and the circular region encompassed by the length of the longline set. Plots of yellowfin tuna CPUE versus mean circular polygon SST, SST coefficient of variation, mean polygon gradient, and polygon gradient coefficient of variation, respectively, indicated no apparent relationship between CPUE and these statistics (Figs. 10–13, computed for polygons with radii equivalent to set length). This result was also true when examining plots of yellowfin tuna CPUE versus the polygon statistics partitioned by month and percentage cloud cover, and for polygon statistics computed using the more restricted regions encompassed by one half and one quarter of the set length.

Discussion

Although the results of other studies support the hypothesis that tuna are more abundant near thermal fronts (Laurs et al. 1984, Maul et al. 1984, Fiedler and Bernard 1987), we were unable to detect any relationship between yellowfin tuna CPUE and SST structure in the northwestern Gulf of Mexico during 1986–87. Our results therefore seem to contradict, at least for the northwestern Gulf of Mexico, the belief among longline fishermen that tuna and other oceanic fish aggregate in regions of rapid temperature change. The perception of increased fishing success near fronts has apparently been incorporated into the fishing strategy used by the longline fleet, since fishermen monitor SST and other environmental indicators to decide where to set the gear. However, our data represent the initial stages of this developing fishery, and the longliners may have employed this strategy in the absence of alternative information concerning where best to locate their gear.

We nonetheless accept that under appropriate circumstances, oceanic fish orient to and aggregate at thermal features. Hence, there may be several explanations why we did not detect any associations. Only one set of geographic coordinates was recorded for each longline set, and it was not known whether the location represented the beginning, midpoint, or end of the set. By comparison, the positive albacore-front associations reported by Laurs et al. (1984) were obtained using data from trolling vessels. In that case, fishing effort could be located more precisely, both in terms of the fisherman's strategy and with respect to analyzing the resultant CPUE relative to SST patterns. Since longlines used by the Gulf fleet may exceed 50 miles in length, the uncertainty associated with the unknown orientation of the set could have masked a relationship between yellowfin tuna CPUE and the satellite-derived SST structure. Although the actual orientation of a set would be difficult to determine, given the effects of wind and currents during the time the gear was fished, information on the coordinates of each end of the longline during payout and haulback would provide some insight into the spatial orientation of the set, and in turn enable a more refined analysis of tuna-temperature associations. Finally, information on the times of payout and haulback would be valuable for refining estimates of fishing effort and selecting satellite images nearer the actual times of fish capture.

An alternative analytical approach would be to define specific fronts in the imagery, and examine CPUE versus distance from an identified front as the measure of the association between fish and front. This is the

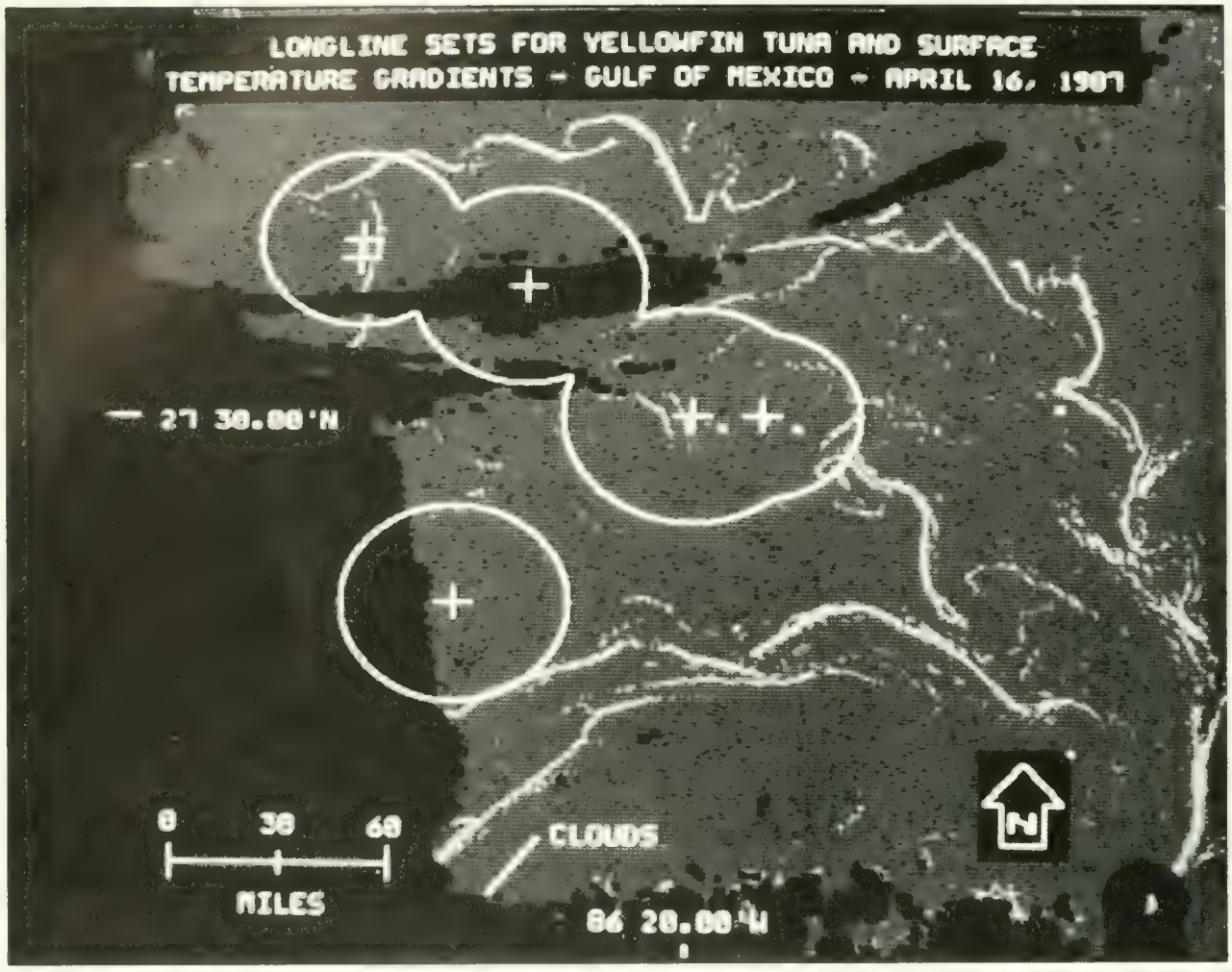


Figure 9

Example of sea-surface temperature (SST) gradient image. Lighter colors indicate higher gradient magnitude, as at frontal zones. Crosses indicate locations of longline sets, with circles encompassing length of sets.

approach used by Maul et al. (1984) and others, and may work well if the interest is in a dominant and clearly defined feature such as an edge of the Loop Current or the Gulf Stream. We did not use this approach for two reasons. First, the additional time and computational effort seemed unwarranted, based on the negative outcome of our gradient analyses. Secondly, such an approach would require us to define a "front" using an arbitrary criteria: we would necessarily have to define a given gradient magnitude, extending over a given distance, as comprising a suitable front. Then, because we would expect to define multiple fronts in the northwest Gulf of Mexico (cf. Fig. 1), defining distances to the fronts would be problematic. For example, in the case where a longline set was located 40km from one of the defined fronts, and 60km from another, it would be difficult to determine to which front the set should be related. Additionally, elevated catches near a front do not necessarily indicate fish were directly associated with that front; animals proximal to a front have not necessarily reacted to its existence. We believe our approach, which asks, "Are catches elevated when SST varies over some region encompassing those catch locations?", to be a more conservative and objective assessment of possible fish-SST associations. It is also one less likely to be inadvertently biased by preconceptions concerning fish-front associations.

There are also several possible biological explanations why we did not find a tuna-temperature relationship:

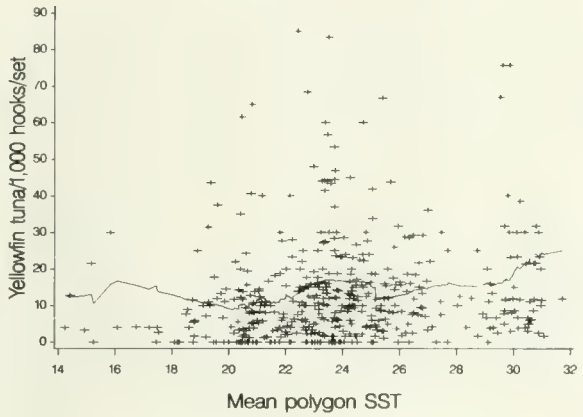


Figure 10
Yellowfin tuna CPUE versus corresponding satellite-derived sea-surface temperature (SST) in the circular region equivalent to longline set length. Curve is fit using robust locally-weighted regression.

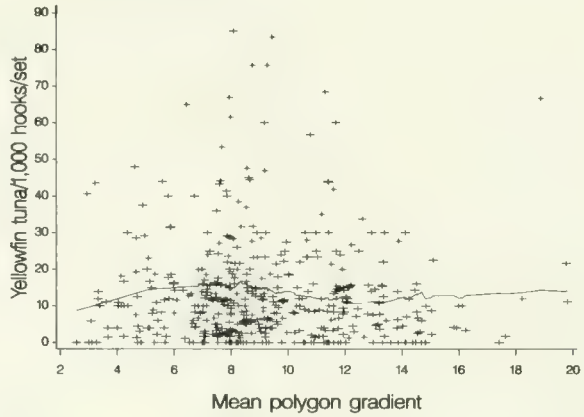


Figure 12
Yellowfin tuna CPUE versus corresponding satellite-derived sea-surface temperature (SST) gradient in the circular region equivalent to longline set length. Curve is fit of data using robust locally-weighted regression.

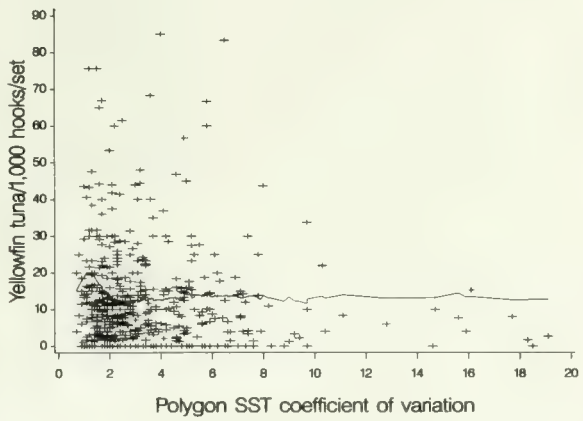


Figure 11
Yellowfin tuna CPUE versus corresponding satellite-derived sea-surface temperature (SST) coefficient of variation in the circular region equivalent to longline set length. Curve is fit of data using robust locally-weighted regression.

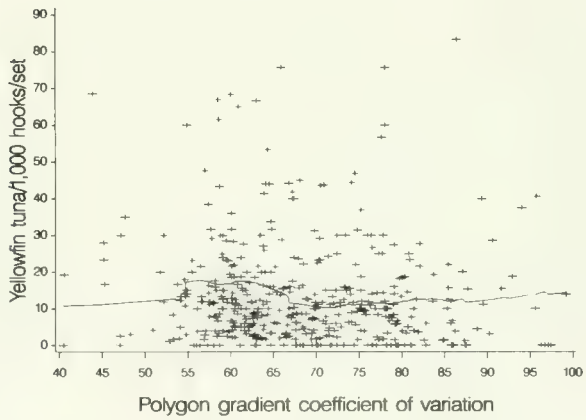


Figure 13
Yellowfin tuna CPUE versus corresponding satellite-derived sea-surface temperature (SST) gradient coefficients of variation in the circular region equivalent to longline set length. Curve is fit of data using robust locally-weighted regression.

(1) Tunas are renowned for their swimming ability, and telemetric studies have demonstrated that 70 cm skipjack tuna can readily traverse a distance of over 100 km/day (Dizon et al. 1978). Although yellowfin tuna in this study may have remained in the vicinity of a particular front for an extended period, it is also possible the yellowfin tuna were actively moving over a wide geographic area. (2) The particular longline set may have been targeting other species, and so hooks may have been set at a depth or time of day inappropriate for the capture of yellowfin, also masking any yellowfin CPUE-temperature relationships. (3) There is some evidence that yellowfin tuna aggregate at fronts during certain life-history stages. Beardsley (1969) compared numbers of yellowfin tuna caught by longlines, purse seines, and bait boats at a frontal zone in the eastern tropical Atlantic. He concluded that the smaller surface-schooling yellowfin taken in the purse seines were more abundant near the front, but that there was no apparent association between the front and the numbers of larger fish captured on longlines. Additional biological information such as length, sex, gonad

weight, maturity stage, and age is necessary to determine whether relationships exist between frontal occurrence and life-history stages of the species. Also, yellowfin tuna may aggregate at color fronts, and not thermal boundaries. This phenomenon was observed by Laurs et al. (1984) in albacore tuna.

Finally, the SST structure present in the northwest Gulf of Mexico is dynamic, and can change rapidly depending on local atmospheric conditions. Huh et al. (1978) provide a sequence of Gulf of Mexico images demonstrating how SST can change with time, and speculated that air-sea heat fluxes can rapidly alter the pattern of SST temperatures observable from satellites. The AVHRR detect only the immediate surface temperature (Schluessel et al. 1987), which may not be indicative of deeper water the yellowfin tuna may prefer. Consequently, the surface thermal patterns in the northwestern Gulf of Mexico may not persist long enough to either aggregate yellowfin tuna directly or set up other conditions, such as enhanced food availability, that would result in a detectable fish-temperature relationship.

In summary, the fisherman's belief that tuna aggregate in response to thermal patterns is a persuasive argument that such behavior occurs, and we initiated this research with that preconception. We are now uncertain whether such a phenomenon has global applicability, and consider from our results that this behavior does not reliably occur in the northwestern Gulf of Mexico. This may be due to the dynamic and non-persistent nature of the thermal patterns, or that those patterns do not generally occur in conjunction with other processes such as upwelling.

Acknowledgments

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Abstract.– Otolith microstructure analysis was applied to sagittae from 18 larvae (5–10 mm notochord length) and 77 juvenile, young adult, and adult (4.3–212 cm lower jaw fork length, LJFL) Atlantic blue marlin *Makaira nigricans* for estimation of age and growth rate. Contingency table analyses indicated that a periodicity of one increment per day was most consistent with the seasonal distribution and peaks of back-calculated spawning dates of the aged samples (May to November), and with information on spawning reported in the literature. Microstructural features of larval blue marlin sagittae were indistinguishable from those in the otoliths of other tropical pelagic species where conclusive age validation has verified daily increment deposition rates. Average percent error of the counting method (precision) for the aged samples of juveniles and young adults/adults was 1.6%.

Estimated ages of larvae ranged from 9 to 12 days while estimated ages of juveniles, young adults, and adults ranged from 21 to 495 days (1.4 years). Otolith microstructure analysis could not be applied with confidence to blue marlin older than 1.4 years. Allometric equations for the length-weight relationship of immature (≤ 140 cm LJFL) and mature male and female blue marlin (>140 cm) are presented. Sexual dimorphic growth (weight only) in Atlantic blue marlin appears to begin at 140 cm LJFL.

Both the maximum (~16 mm/day at 50 days) and sustained (~10 mm/day) growth rates in length during the first 100 days indicate that Atlantic blue marlin are one of the fastest growing of all teleosts in the early stages of development. An attempt to determine the periodicity of presumed annual marks on otoliths from adult blue marlin (213–367 cm LJFL) by evaluating microstructural characteristics and increment counts between annuli was unsuccessful.

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Estimating Age and Growth of Young Atlantic Blue Marlin *Makaira nigricans* from Otolith Microstructure

Eric D. Prince
Dennis W. Lee
James R. Zweifel

Miami Laboratory, Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA
75 Virginia Beach Drive, Miami, Florida 33149-1099

Edward B. Brothers

EFS Consultants, 3 Sunset West, Ithaca, New York 14850

Published reports on age determination for billfishes (Istiophoridae) are rare compared with those available for other fishes (Lee 1989). Moreover, data providing validated ages for this family are almost nonexistent (Prince et al. 1987), yet age and growth data are important for stock assessment of fish populations (Beamish and McFarlane 1983).

Age determination of Atlantic blue marlin *Makaira nigricans* is probably more difficult than for most other teleosts because of numerous aspects of the marlin fishery and their life history, including the facts that (1) their life cycle does not lend itself to artificial propagation or survival in captivity, (2) they are a very large, highly mobile, solitary, comparatively rare, and sparsely distributed predator with an extensive geographical range, making them inaccessible for routine scientific study and increasing the costs and difficulty of obtaining samples, (3) they occupy different climatic areas during the same calendar year, making interpretations of bands on hard structures less certain because they may not form with great regularity or uniformity, (4) while incidental catches from longline fisheries form the largest part of their harvest, the logistics of sampling longline operations have hindered collection and examination of large numbers for scientific study, (5) in comparison with almost all other teleosts, their otoliths are exceptionally small and fragile, making them difficult to extract and expensive to prepare and analyze, (6) specimens less than 34 kg (75 lb) are extremely rare, due in part to the apparent exceptionally rapid growth rate in juveniles, (7) extremely low tag-recapture rates (0.4% in the Atlantic; Scott et al. 1990) make acquisition of hard structures from long-term recaptures or oxytetracycline injected blue marlin highly unlikely, and (8) long-lived species are more difficult to age and preliminary indications suggest that blue marlin are long lived, attaining ages of 25–30 years or more (Hill et al. 1989).

Recognizing these difficulties, the National Marine Fisheries Service's (NMFS) Southeast Fisheries Science Center (SEFSC) began a long-range plan in 1980 to collect samples for age determination and an evaluation of ageing methods of blue and white

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marlin *Tetrapturus albidus*. An initial report (Prince et al. 1984) indicated that otoliths and dorsal spines were the most promising structures examined, but the best approach for determining the accuracy of these two ageing methods was unclear. Marginal increment analysis (MIA) of 328 dorsal spine sections (Prince et al. 1987) failed to provide evidence of the temporal periodicity (i.e., regularity) of annulus formation, due in part to the large amount of variability in these measurements.

Estimates of age and growth rates of young fish are generally more reliable than for adults because microstructural increments on otoliths of fast-growing juveniles are fewer in number and are often easier to count or measure accurately (Casselman 1983, Prince et al. 1987, Summerfelt and Hall 1987). In addition, otolith microstructural analysis for ageing young fish is inherently more precise than counts of annual marks on structures of adults since errors in counting increments are made in days, not years. Following the recommendations of Prince et al. (1987), otolith microstructural analysis of young blue marlin was selected as the method of choice for improving knowledge of age and growth of this species. The small otoliths, narrow increment widths, and longevity of blue marlin (25–30 years) were expected to limit the microstructural method to the first few years of life. A few researchers, however, have reported success in counting microstructural increments between presumed annual marks on sagittae from older adult temperate and tropical species (Pannella 1971, Radtke 1984, Brothers and Mathews 1986) as a means of determining their periodicity in older fish.

Objectives of this study were to (1) estimate the age and growth of young Atlantic blue marlin from otolith microstructural analysis, (2) determine the periodicity of increment formation by (i) comparing the distribution of back-calculated spawning dates with the spawning season of Atlantic blue marlin reported in the literature, and by (ii) comparing microstructure characteristics of increments on larval blue marlin otoliths with those found in other species where increment deposition rate has been established, (3) determine the precision of the ageing method, (4) fit the ageing data to an appropriate growth equation(s) so daily growth rates could be compared with other fast-growing species, and (5) determine whether counts of microstructural increments between presumed annuli in otoliths of adult blue marlin are consistent with the hypotheses that microstructural increments are deposited daily and gross zonation is annual.

Methods

Data used in this study cover several distinct life-history stages, i.e., larvae, juveniles, young adults, and adults. Although our life-history partitions are somewhat arbitrary, they are defined here to minimize confusion related to their use in various analyses described below. All references to length for juvenile, young adult, and adult blue marlin in the remainder of the paper are lower jaw fork length (LJFL), while length for larvae are notochord (NL) or standard length (SL). Adults were separated from younger stages at about 110 cm, based on changes in form of the length-at-age relationship (discussed later). All planktonic blue marlin larvae in our sample were <11 mm. Juvenile blue marlin 4.3–110 cm were always sexually immature and did not have the full array of adult morphological characters. A few young adult blue marlin >110–140 cm had the full array of adult morphological characteristics but most in this size range were sexually immature. Sexually mature adult blue marlin were nearly all over 140 cm and had the full array of adult morphological characteristics.

Data collection

Juveniles, young adults, adults During 1980–83, juvenile through adult Atlantic blue marlin were collected directly by NMFS samplers from taxidermists, commercial and recreational fishermen, and at billfish tournaments or ports in the Gulf of Mexico, Caribbean Sea, and northwestern Atlantic Ocean. All size categories were initially targeted and 3–5 hard structures, including sagittae, were collected from each specimen. After 1983, a special "save it for science program" was developed (Prince 1984) to obtain extreme size categories, since blue marlin under 100 pounds (45 kg) and over 900 pounds (409 kg) are very rare in the northwestern Atlantic Ocean (Prince et al. 1984).

Most blue marlin specimens used in this study were caught on hook-and-line, but dipnets were also used for smaller size categories. In addition, some specimens were obtained from the stomachs of larger predators. Fish samples were preserved by freezing or immersion in 95% ethanol to reduce deterioration of the otoliths.

When possible, the following supplemental data were collected from each fish: (1) lower jaw fork length, (2) round weight, (3) sex, and (4) date of capture. Length measurements along the contour of the body were made to the nearest centimeter (cm). Weight was measured to the nearest pound and later converted to kilograms (kg). Sex was determined by visual inspection or histological examination (M.J. Wolfe, Dep. Avian and Animal Medicine, Cornell Univ., Ithaca, NY

14853-6401, pers. commun., 14 Aug. 1987). When sex could not be determined, specimens were designated as unknown sex. Otoliths (sagittae) were removed from the craniums using extraction procedures of Radtke (1983a).

Larvae Istiophorid larvae were collected 25–26 August 1982 at 14 stations off Miami, Florida, during a two-day cruise of the *RV Virginia Key*. Surface tows were made at the western edge and in the axis of the Gulf Stream using either a 1 m conical plankton net or a 1 × 2 m neuston sampler, both with 0.947-mm mesh size. Larval istiophorids were separated from the other plankton, and their numbers represented about 5% of the fish in the samples. All larval samples were preserved in 95% ethanol.

Preserved istiophorid larvae were soaked in water for several minutes before measurements were recorded and otoliths extracted. This reduced some of the shrinkage caused by the alcohol and tended to straighten and soften the bodies. Theilacker (1980) reports that shrinkage of larvae caused by net-handling decreases with size while that due to preservation alone is constant. Since all the larvae were nearly the same size (5–10 mm), we assumed shrinkage to be an undetermined constant proportion.

Larvae were measured with a dissecting scope to the nearest 0.1 mm from the tip of the lower jaw to the tip of the notochord (NL), or to the developing hypural plate (SL). Otoliths were removed from larvae using the methods of Brothers and McFarland (1981). Istiophorid larvae were then cleared and stained according to methods of Potthoff (1986) so vertebral counts could be made. The blue marlin larvae were distinguished from the *Istiophorus–Tetrapturus* group based on vertebral counts.

Otolith preparation and microstructural analysis

The general approach of Brothers et al. (1983) for otolith microstructure analysis of larval and juvenile bluefin tuna was adopted for this study. Otolith mass for all blue marlin ≥4.3 cm was measured on a microbalance to the nearest 0.01 mg. The extremely small size of sagittae from blue marlin ≤4.3 cm precluded measurements of otolith mass for this size category. The transparency and shape of otoliths from larvae and small juveniles (≤23 cm) allowed their examination, without further preparation, with a compound light (polarized) microscope adapted for video viewing. Because of the change in mass and configuration of sagittae from larger fish (≥23 cm), preparation of these otoliths included breaking them along the sulcus by light pressure with a scalpel. The medial surface of the dorsal lobe was ground on a glass plate with a mineral oil slurry of 600-grit silicon dioxide to slightly thin the fragment and give it a flat surface on which to rest. The distal surface was then ground with the 600-grit to a point just short of reaching the core region of the otolith. Fine emery paper or diamond compound (3 μm) was then used to polish the surface.

The best counting paths were found to be on either the anterior (antirostrum) or posterior axis of the dorsal lobe (Fig. 1A). Counts and photographs of the video image of "primary" microstructural increments (Geffen 1987) are from the dorsal lobe and, where possible, along the anterior axis (Figs. 1B–D). Alternatively, due to lack of specimen clarity or poor preparation, counts were made along the posterior axis. Counts started at the first visible increment outside the core (Fig. 1C) and continued to the margin of the structure (Fig. 1D). Increment counts and measurements were made at magnifications ranging from 100 to 2500 ×.

Increment counts for larval, juvenile, and young adult/adult blue marlin otoliths include only primary increments. Fine increments, provisionally identified as "subdaily" (Figs. 2A, B), were often observed in the otolith region corresponding to larval and early juvenile growth. These subdaily increments were easily identified by their vague appearance and regular clustering within the more prominent primary units (Fig. 2), and were not tallied.

Counts were not corrected for age at first increment formation because known age larvae were not available. Back-calculated spawning dates were computed by subtracting the total count of primary increments for each sample from the date of capture.

Preparation of otolith sections for scanning electron microscope (SEM) examination followed methods described by Brothers et al. (1983), Brothers and Mathews (1986), Brothers (1987), and Jones and Brothers (1987). Some otoliths were sectioned and rough polished according to the methods of Wilson (1984). The majority of increment counts were made on lateral views of whole otoliths or broken sagittae, but a limited number of samples (9) were available in which counts could be made from transverse sections and whole sagittae from the same fish.

Otoliths that were found to be overground, eroded, decalcified, or which had an irregular, disrupted, or unusual microstructural record were excluded from the ageing analysis.

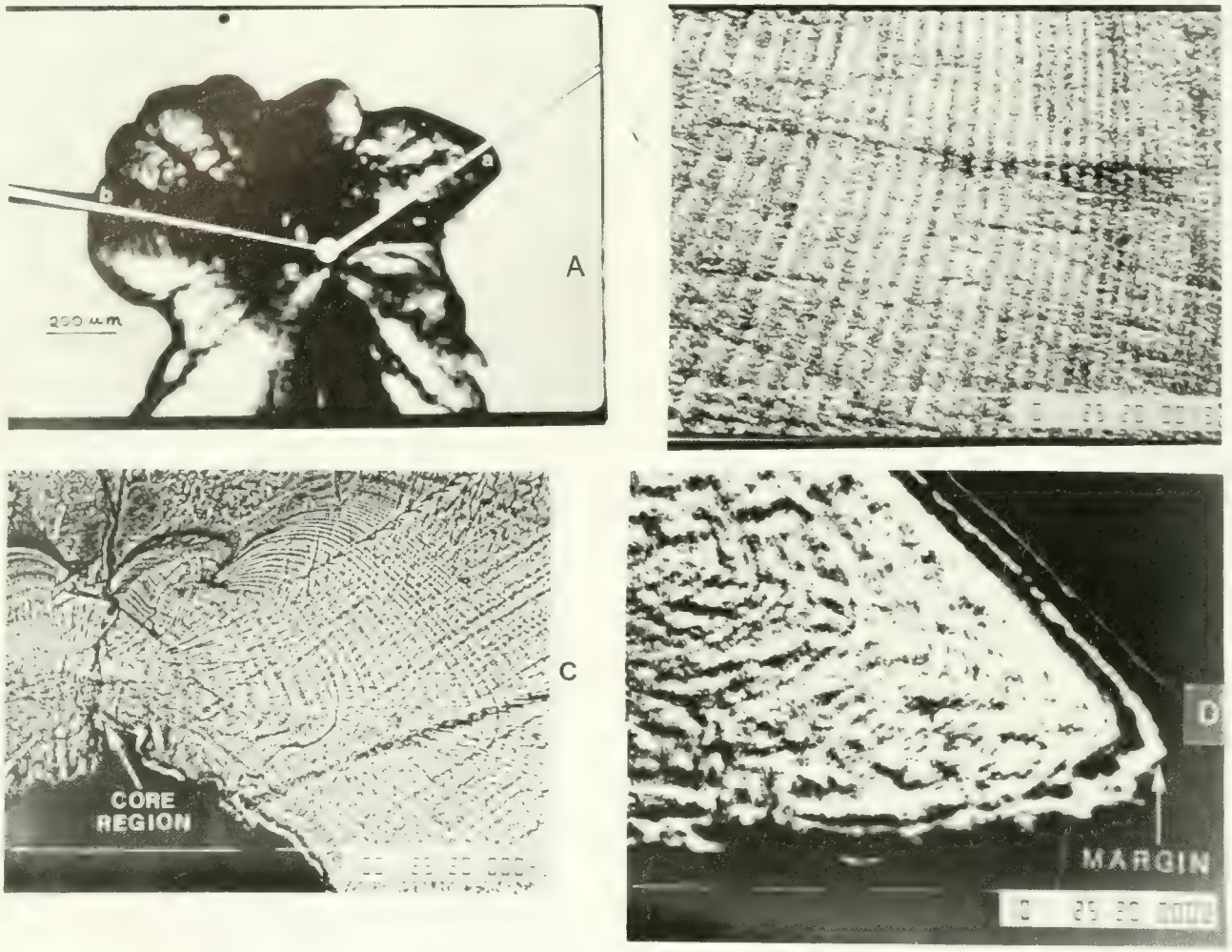


Figure 1

Juvenile Atlantic blue marlin *Makaira nigricans*. (A) Photomicrograph of the video image of a whole otolith. White lines indicate the preferred counting paths on the anterior (a = antirostrum) or posterior (b) axis of the dorsal lobe of the sagitta. Black bar = 200 µm. (B) Primary increments formed during the first few months of life in a sagitta from a 139.7 cm LJFL specimen. White bar = 10 µm. (C) General location of the core on a sagitta from a 136.6 cm LJFL specimen. White bar = 100 µm. (D) Location of the margin of the antirostrum on a sagitta from a 139.7 cm LJFL specimen. White bar = 10 µm. B–D are SEM micrographs of transverse sections.

Precision of age-determination technique

The repeatability or precision of otolith microstructural analysis applied to juveniles and young adults/adults (for increment counts 21–495) was assessed using the average percent error (APE) approach of Beamish and Fournier (1981). Three nonconsecutive blind counts were made by the same reader. Computation of APE for individual samples was:

$$\mathrm{APE} = 100\left(1/\mathrm{R}\left(\sum_{i=1}^{R}|\mathrm{X_{ij}} - \mathrm{X_j}|/\mathrm{X_j}\right)\right) \qquad (1)$$

where X_{ij} = the ith count for the jth fish, X_j = the average count for the jth fish, and R = the number of counts for each fish.

The index of APE for all fish in this sample (N 77) using a single reader was:

$$\mathrm{APE} = 100\left(1/\mathrm{N}\left(\sum_{i=1}^{N}\left(\mathrm{I}/\mathrm{R}\left(\sum_{i=1}^{R}|\mathrm{X_{ij}} - \mathrm{X_j}|/\mathrm{X_j}\right)\right)\right)\right) \qquad (2)$$

where N = the total number of juvenile and young adults/adults aged.

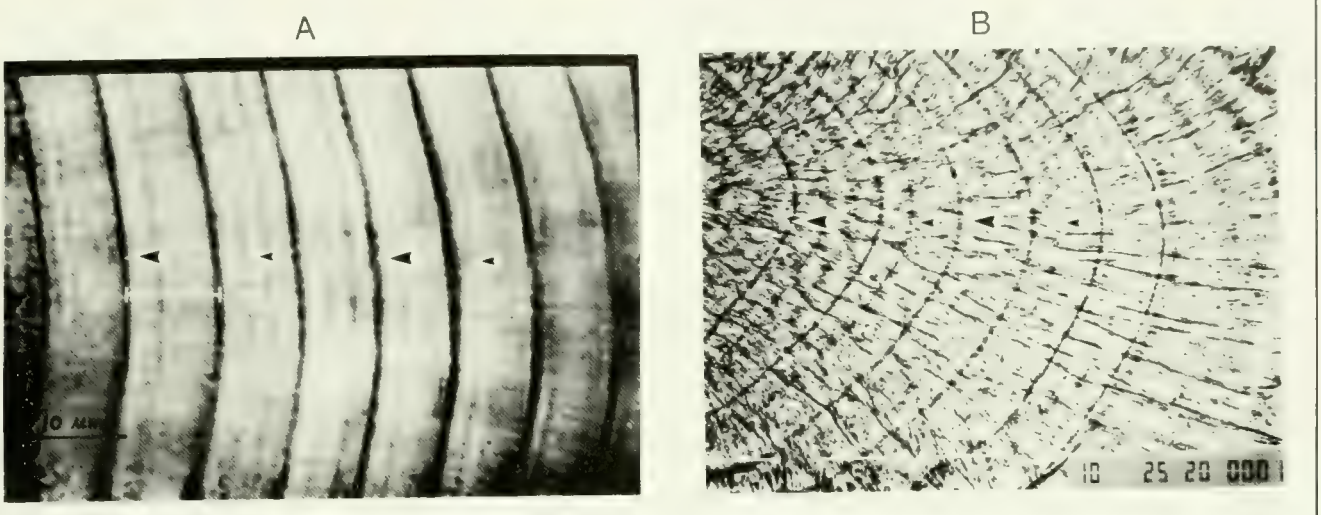


Figure 2
(A) Photomicrograph and (B) SEM micrograph of the video image of primary (between large arrows) and subdaily (small arrows) increments in a whole sagitta from a 178 cm LJFL Atlantic blue marlin *Makaira nigricans*. Black bar = 10 μm.

Computations of APE were not made for the 18 larval blue marlin because only one count was made for each of these samples.

Statistical procedures

Length-at-age The growth trajectory for the age range in our sample, as summarized in Table 1, is asymmetric and S-shaped, with growth rates increasing up to about 40–50 cm and declining thereafter. Richards (1959) described the relationship between this inflection point (relative to the maximum or asymptotic size) and the most common growth equations. The von Bertalanffy equation has no inflection point and those for the Gompertz and logistic equations are at 3/8 and 1/2 of the maximum size, respectively. In addition, the logistic equation is symmetric around the point of inflection.

The Gompertz equation was appropriate for modeling growth of younger fish (i.e., it had an inflection point and was asymmetric). Assuming an inflection point of 40 cm and dividing by 3/8, we estimated a maximum size of 107 cm for this growth phase. In order to obtain a better estimate of limiting size for this growth stanza, we included data up to 113 cm (111 days) and fit the Gompertz equation

$$L = P_1 * \exp\{-P_2 * \exp[-P_3 * t]\} \qquad (3a)$$

to data for young fish. This procedure allowed us to assess the upper and lower limits of each growth equation (i.e., above and below 110 cm).

We used the von Bertalanffy equation

$$L = P_1 * \{1 - \exp[P_2 * (t - P_3)]\} \qquad (3b)$$

for older fish, including data down to 95 cm (96 days), since no inflection point was evident in this range. Results using the two equations differed by less than 2 cm at 110 cm body length, and growth rates were nearly the same at this length. Therefore, data were separated at 110 cm for subsequent analyses. Combining these two equations provides continuous estimates of size-at-age and daily growth rates for the age range in our data.

Generic parameter labels (P for length, Q for weight) are used in growth equations to indicate that no physical or biological meaning should be ascribed. In general, growth equation parameters are highly intercorrelated and, in addition, are highly correlated with the size range of the data. Our data covers only the initial phase of adult growth, so the usual biological and temporal interpretations are unwarranted. For the same reason, the use of generalized or multicycle equations did not seem appropriate.

Least-squares estimates of the parameters of the von Bertalanffy and Gompertz equations were obtained using Marquardt's (1963) algorithm and the methods of Conway et al. (1970). Because the size range in our data covers fish from 5 mm to over 212 cm, the natural log transformation was used to minimize proportional rather than absolute differences.

Table 1

Summary of results of the otolith microstructure method applied to sagittae of Atlantic blue marlin *Makaira nigricans*. Range in estimated age (days), sample size (n), mean increment count (days), mean observed and estimated (in parentheses) lower jaw fork length (LJFL, cm), average growth rate (cm/day), LJFL range (cm), mean observed and estimated (in parentheses) round weight (kg), and round weight range (kg) are given for each age category. Estimated lengths and weights were computed from growth equations described in text.

Range in estimated age (days)	Sample size (n)	Mean increment count (days)	Mean LJFL (cm)	Average growth rate (cm/day)	LJFL range (cm)	Mean round weight[1] (kg)	Round weight range (kg)
1–20	18	10	[2]0.6 (0.7)	0.1	[2]0.5–1.0	–	–
21–30	1	21	4.3 (3.9)	0.3	4.3	[3]0.6 (0.4)	[3]0.6
31–60	1	40	23.0 (23.1)	1.0	23.0	0.1 (0.1)	0.1
61–90	1	89	95.3 (91.3)	1.5	95.3	4.3 (4.7)	4.3
91–120	7	105	103.3 (102.3)	0.5	88–118	6.2 (6.6)	3.5–10.0
121–150	3	141	114.7 (119.0)	0.3	100–126	9.6 (12.1)	8.4–11.4
151–180	5	169	128.5 (129.5)	0.5	116–136	13.5 (15.1)	10.9–17.5
181–210	9	193	143.9 (137.2)	0.7	129–173	17.5 (17.9)	12.7–21.8
211–240	7	229	147.4 (147.6)	0.1	139–152	24.5 (22.6)	19.5–39.0
241–270	4	254	161.8 (153.9)	0.6	150–172	30.5 (26.1)	20.0–43.1
271–300	5	292	158.8 (162.3)	−0.1	153–173	30.7 (31.9)	22.7–45.8
301–330	7	317	156.9 (167.3)	−0.1	140–170	30.1 (36.1)	24.0–36.3
331–360	4	341	170.6 (171.4)	0.6	149–180	43.6 (39.9)	38.5–47.2
361–390	9	373	172.4 (176.4)	0.1	160–193	40.5 (45.5)	30.8–58.0
391–420	3	411	199.8 (181.4)	0.7	196–207	62.5 (52.0)	51.7–72.4
421–450	8	432	183.1 (184.0)	−0.8	154–196	49.7 (55.8)	35.4–58.0
451–480	2	454	190.9 (186.3)	0.4	173–209	56.1 (59.6)	40.0–72.2
481–510	1	495	212.1 (190.1)	0.5	212.1	83.9 (66.6)	83.9

[1]Mean weight was averaged for males and females >110 days.
[2]Notochord length
[3]Grams

Length-weight relationships Significant changes in body form usually occur at or near sexual maturity for most teleosts. The smallest mature male blue marlin reported in the literature is about 166 cm long (Erdman 1968). However, we established the upper length limit for immature fish at 140 cm because the length-weight relationship of fish between 140 and 166 cm in our sample appeared to be closer to that for larger fish.

Differences in the slopes and Y-intercepts of the length-weight relationships for each sex category (i.e., males, females, and unknown sex) were tested using covariance analysis. Mature fish in our age analysis are a small and size-selected subsample of those available, since a majority of the adult blue marlin population is over 200 cm. To maximize the amount of information for length-weight analysis of mature adults (>140 cm long), we used all available length and weight data collected by the SEFSC recreational billfish survey program from 1972 to 1988 (1969 males, 3260 females). Covariance analysis was used for fish in the common length range 140–277 cm (maximum length of males in the sample) to compare the length-weight relationship of mature male and female blue marlin. Separate length-weight equations were developed for the entire mature size range of both sexes, and a single length-weight equation was used for immature fish (≤140 cm).

Weight-at-age The variability of weight-at-age in our data was large and sample sizes for each sex were small, a common occurrence in marlin studies. Since variability in length is much less than for weight and our length-weight relationships are based upon large numbers of fish, we estimated weight-at-age by converting individual lengths to weights. For larvae and juveniles, we converted parameters of the Gompertz length-at-age equation directly using equations 4a–d below.

From equation 3a and using the allometric equation

$$\ln W = a + b \ln L,$$

we obtain

$$\ln W = a + b * \ln P_1 - b * P_2 * \exp[-P_3 * t]$$

which allows us to derive the weight-at-age equation

$$W = Q_1 * \exp\{Q_2 * \exp[-Q_3 * t]\} \quad (4a)$$

where

$$Q_1 = \exp(a) * P_1 * * b \quad (4b)$$

$$Q_2 = b * P_2 \quad (4c)$$

and

$$Q_3 = P_3. \quad (4d)$$

Gompertz equations were used to describe the age-weight relationship for all sizes of blue marlin in this study. For larvae and juveniles, we converted the length parameters (P) to weight parameters (Q) directly using equations 4a–d. For adults, we first converted individual lengths to weights using either the equation for immature fish for young adults (see Results) or the sex-specific equations (see Results) for fish larger than 140 cm and then fit the Gompertz equation (4a) to obtain a continuous young adult/adult weight-at-age relationship.

Increment counts Spearman's rank correlation (SRC; Conover 1971) was used to evaluate the association of total increment count with LJFL, otolith weight, and round weight. Chi-square contingency table analyses (Snedecor and Cochran 1980) were used to determine whether the distribution of back-calculated spawning dates was independent of predicted deposition rates (with periodicities (P) of 0.1–0.9, 1, and 2 increments per day) and days to first increment formation. Fractional periodicity values are interpreted as the proportion of increments actually counted; i.e., true age is underestimated. Multiple increments per day would correspond to overestimates of age, possibly due to counting subdaily increments. To minimize the effect of small sample sizes in a cell, spawning dates were tallied by calendar quarters for each periodicity (P) value. Because all larvae were collected within a 48-hour time period, only the average larval age and length were used in these calculations.

Results

Limitation of the ageing method

Otolith analysis Sagittae from 155 juvenile, young adult, and adult blue marlin, ranging in length from 4.3 to 369 cm LJFL, and 18 larvae, 5–10 mm NL, were used to test for diel periodicity of increment deposition. References here to increments, primary increments, or daily increments generally imply daily deposition (see Discussion).

The decision to analyze increment counts using the whole otolith method (except for the 18 larval otoliths) was based on our evaluation where both the whole and sectioned otoliths were available from nine specimens. Counts using the whole otolith method were higher in eight out of the nine (88%) sagittae samples analyzed. We felt that the differences were due to the compressed incremental record on sectioned sagittae, and as a result we concluded that section counts consistently underestimated the total increment count. Therefore, we used whole sagittae counts in our analysis.

The otolith microstructure method could not be applied with confidence to whole sagittae from fish longer than 212 cm because of the limitations of light microscopy and difficulties in discriminating finely-spaced increments of less than about 1 μm. Discontinuities of the microstructural record usually occurred at counts of about 400–500 along the antirostrum dorsal lobe counting path. The SEM micrograph in Figure 1B and the entire microstructural record from a 23-cm juvenile illustrated in Figure 3 are examples of the undisrupted incremental record observed on whole sagittae in young fish.

Otolith microstructural analysis was successfully applied to 18 larvae and 77 juvenile and young adult/adult blue marlin. Forty additional blue marlin <212 cm in length (30%) could not be aged using the otolith microstructural method. These samples included otoliths broken or lost during preparation and poorly sectioned otoliths from another study. Therefore, the 30% rejection rate is conservative in estimating the expected yield of useful counts and age data from a fresh set of samples.

Range in estimated age Estimated ages, based on counts on the whole sagittae of the 18 larval blue marlin, ranged from 9 to 12 days (Table 1); 66% of the larvae had either 10 or 11 increments. The range in estimated ages of the 77 juvenile and young adult/adult blue marlin was 21–495 days (a maximum of 1.4 years, Table 1). Correlations between total increment count and round weight (SRC = 0.915), otolith weight (SRC = 0.895), and LJFL (SRC = 0.893) for juvenile and young adult/adult blue marlin were similar or the same.

Periodicity of increment formation

Otolith microstructure Otolith microstructure of larval blue marlin (Fig. 4A) was indistinguishable from that of frigate mackerel *Auxis thazard* and other pelagic species of similar size (Figs. 4B–D). For some species, daily increments have been validated by rearing experiments, otolith marking, or other methods (Brothers et al. 1976, Wild and Foreman 1980, Brothers et al. 1983).

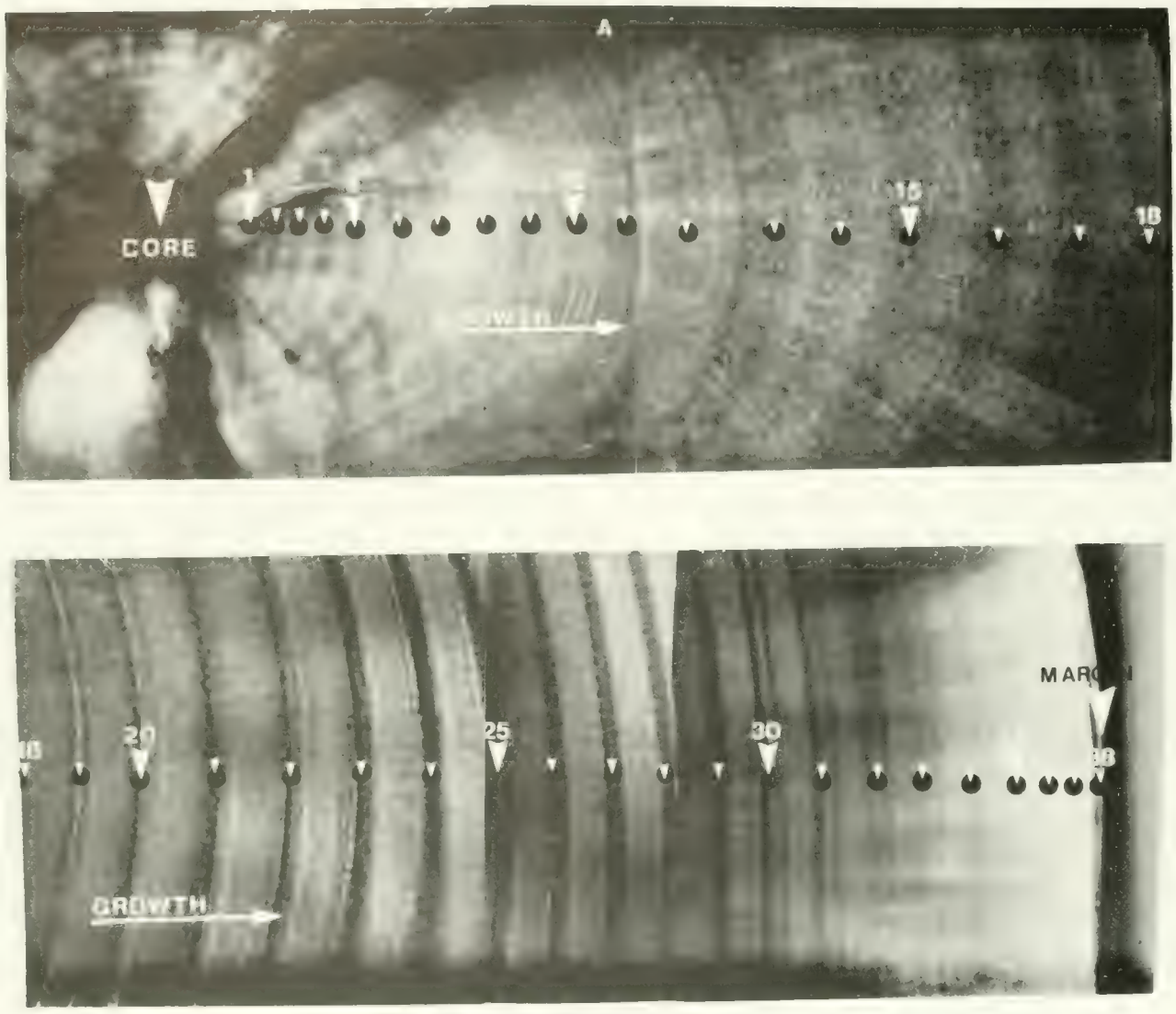


Figure 3

Composite photomicrograph of reader interpretation (E.B. Brothers) of primary increments along the entire counting path of a whole ground sagittae from a 23cm LJFL Atlantic blue marlin *Makaira nigricans*. Location of core, direction of growth, and margin are shown for A (counts 1–18) and B (counts 18–38). Because of problems inherent in sectioning increments on a counting path whose axis of growth is continually changing, mid-increments (20–30) appear in better focus than increments closer to the core and margin. A few increments near the core are not visible in the photograph and thus the total (38) does not match the mean count of three replicate counts (40). Black bar = 10 μm.

An optically dense region (primordium) about 5 μm in diameter comprises the center of blue marlin sagittae and is usually encircled by one or two diffuse, optically dense layers. Well-defined growth increments surround this region. We refer to the area circumscribed by the first clear growth increment as the core (Fig. 1C).

Subunits (optically light and dark rings) of primary increments are of about equal thickness for the first two or three increments. Thereafter the optically translucent subunit becomes progressively wider relative to the denser subunit (Fig. 3). As in other species (Figs. 4A–D), increments on larval blue marlin otoliths appear visibly distinct in nature for most specimens and are structurally analogous to the daily growth increments seen in many other species, including some tropical pelagic species (Brothers 1979, Pannella 1980). Subdaily increments were also observed in blue marlin

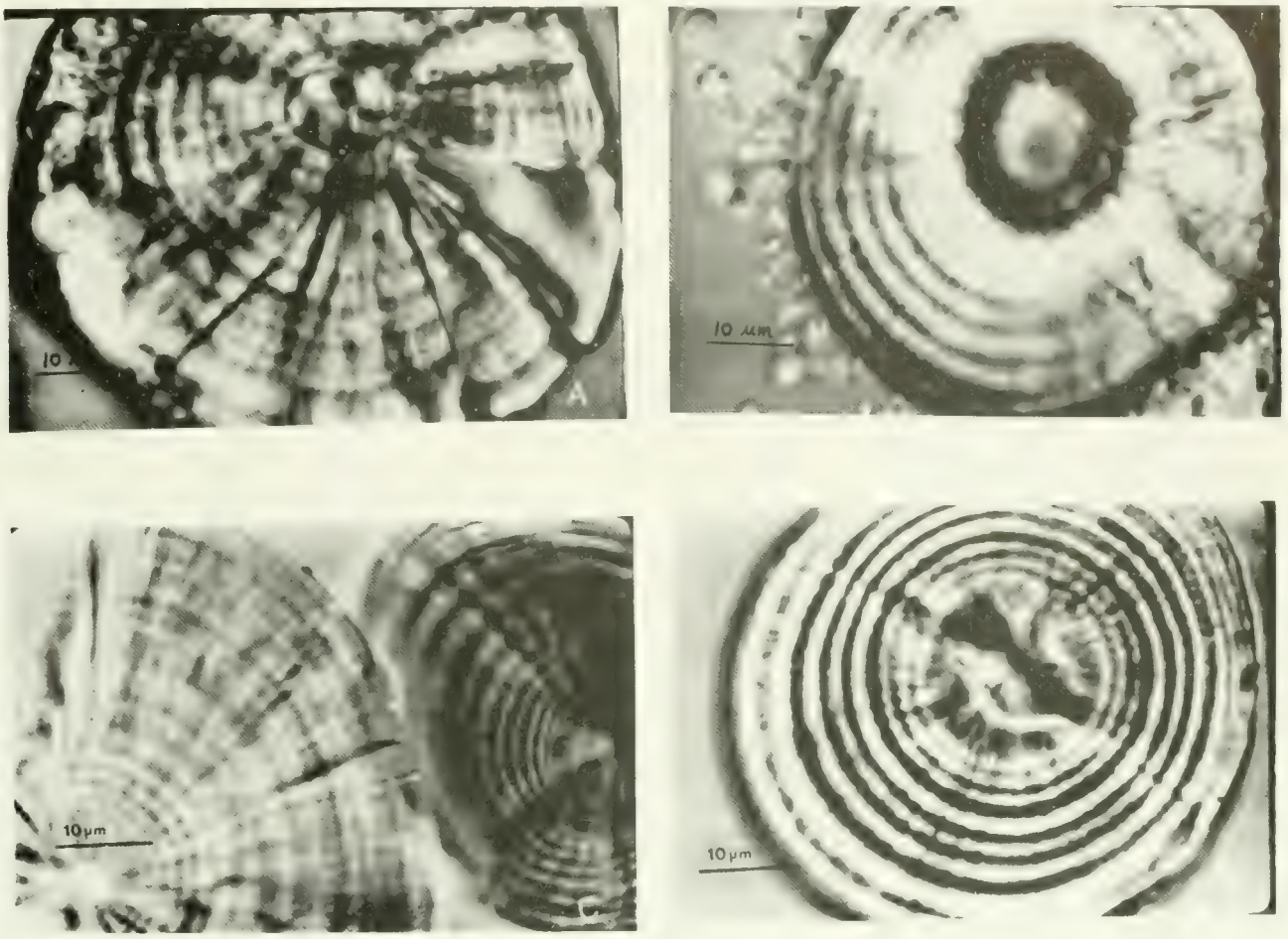


Figure 4

Photomicrographs of the video image of whole otoliths for (A) sagittae from a 5.74 mm NL Atlantic blue marlin *Makaira nigricans* larvae; (B) sagittae from an 8.5 mm NL swordfish *Xiphias gladius* larvae; (C) sagitta (left) and lapillus (right) from an 8.61 mm SL yellowfin tuna *Thunnus albacares* larvae; (D) sagittae from a larval frigate mackerel *Auxis thazard*. Black bars = 10 µm.

otoliths, and have been noted in acetate replicas and SEM preparations of many species, including other oceanic pelagics (Brothers et al. 1983).

Back-calculated spawning dates The primary back-calculated spawning dates (i.e., two or more individuals in a monthly interval) were from May through November (Fig. 5A). Except for the 18 larvae which were all sampled in the month of August, the distribution of back-calculated spawning dates did not appear to be associated with the dates of capture (Fig. 5B). The large variation in age of the juveniles and young adults/adults (about 3–16 months) suggests that calculated spawning dates are not a simple reflection of the distribution of capture dates of size selected fish.

To examine the effect of various increment deposition rates on the distribution of back-calculated spawning dates, we used a contingency table analysis of numbers of spawning dates by season for periodicities (P) of 0.5, 1, and 2 increments per day (Fig. 6A). The distribution of back-calculated spawning dates depends strongly upon the periodicity assumption (χ^2 76.88, df 6, $P<0.0001$). A deposition rate of one increment per day was the only periodicity of those examined that resulted in most spawning occurring in the summer and fall (Fig. 6A). To examine if substantial undercounting of increments occurred, periodicities ranging from 0.1 through 1.0 increments per day were tested (Fig. 6B). Chi-square test for independence (χ^2 85.778, df 24, $P<0.0001$) was highly significant. Only at periodicities

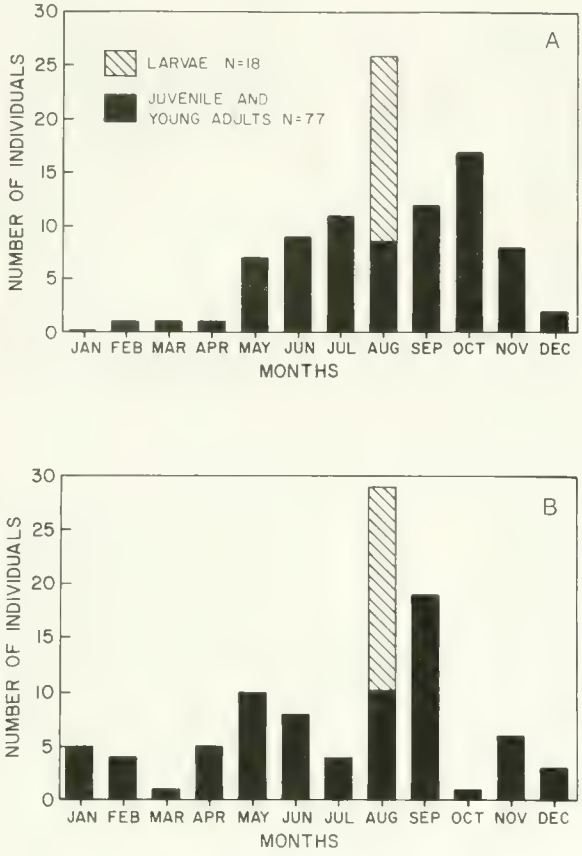


Figure 5

(A) Back-calculated spawning dates for 18 larvae and 77 juvenile and young adult/adult Atlantic blue marlin *Makaira nigricans*. Total increment count on the otolith (sagittae) and date of capture were used to back-calculate spawning month. (B) Distribution of capture dates for 18 larvae and 77 juvenile and young adult/adult Atlantic blue marlin collected 1980–88.

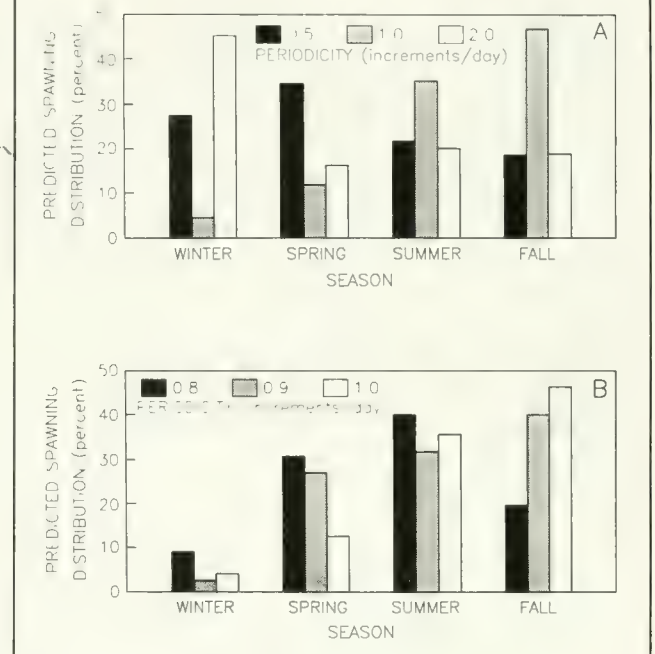


Figure 6

(A) Seasonal distribution of spawning (%) of Atlantic blue marlin *Makaira nigricans* predicted from chi-square contingency table analyses for increment deposition rates of 0.5, 1.0, and 2.0 increments per day, and (B) for deposition rates of 0.8, 0.9, and 1.0 increments per day. Summer and fall spawning is most closely predicted in (A) and (B) by a periodicity of 1.0 increments per day.

of ⩾0.8 do high levels of spawning shift from the second to the fourth quarter (Fig. 6B). A periodicity of 1 increment per day agrees most closely with the qualitative information available for blue marlin spawning activity.

To determine whether the lack of information on the time of first increment formation affected our interpretation of increment deposition rate, we constructed a contingency table of seasonal spawning versus first increment formation of 1–7 days (using a periodicity of 1.0). The Chi-square statistic (χ^2 1.42, df 18, $P>$ 0.999) showed that for P = 1.0, a range of 1–7 days for first increment formation does not significantly alter the back-calculated spawning distribution.

Precision

Average percent error for the aged samples of juvenile and young adult/adult blue marlin (N 77) was 1.6% (Fig. 7). This level of precision is either less than or equal to APE values reported for other species and various ageing methods (Table 2). No obvious trends in APE with the increment count or round weight were evident (Fig. 7). Average percent error generally increased with increases in body length (Fig. 7), except for outliers in the first two lengths of the measured range (4.3 and 23.0 cm).

Length-weight relationships

The length-weight relationship for all immature blue marlin (⩽140 cm; sexes pooled, Fig. 8A), is represented by the allometric equation

$$\ln W = -11.950 + 2.9921 (\ln LJFL); R^2 = 0.98. \quad (5)$$

The length-weight relationships for mature adult blue

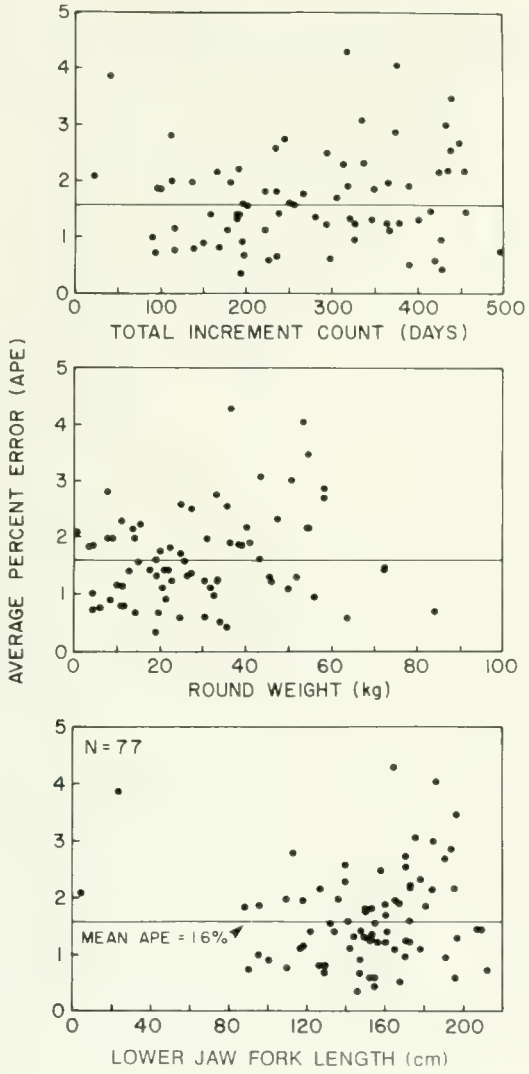


Figure 7

Relationship between average percent error (APE) and (A) total increment count (days), (B) round weight (kg), and (C) lower jaw fork length (cm) for 77 juvenile and young adult/adult Atlantic blue marlin *Makaira nigricans*. Horizontal line indicates mean APE for all samples.

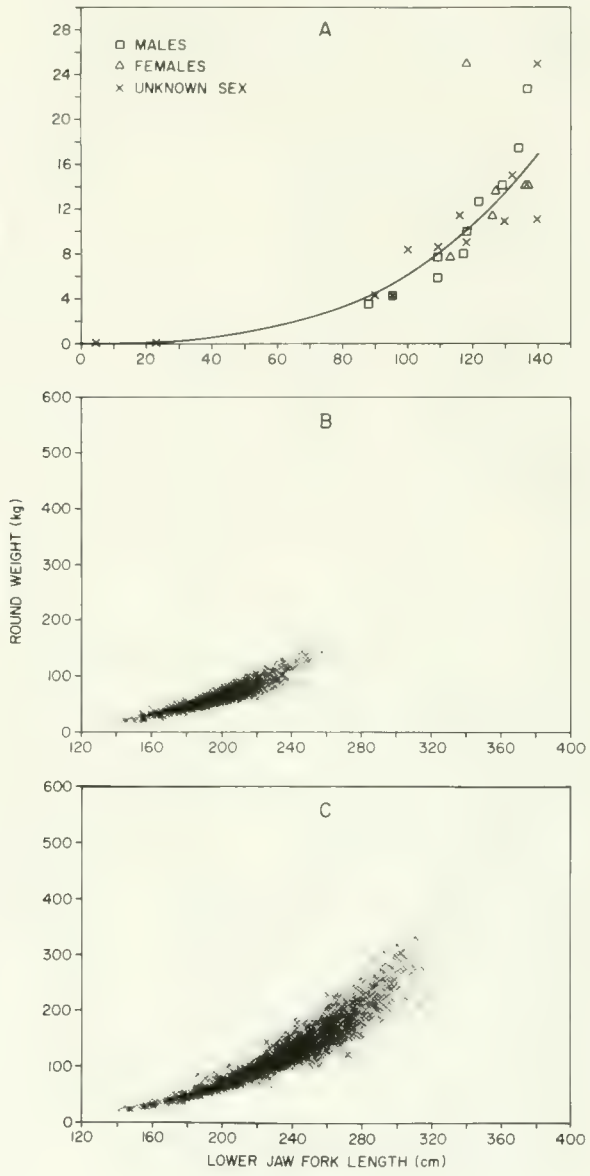


Figure 8

Length-weight relationships for (A) male, female, and unknown-sex juvenile and young adult/adult Atlantic blue marlin *Makaira nigricans*, (B) mature male (>140–277 cm long), and (C) mature female (>140–369 cm long). Sample sizes are 28 for (A), 1969 for (B), and 3260 for (C).

marlin >140 cm (Figs. 8B,C, respectively) are given by the allometric equations

males:

$$\ln W = -12.568 + 3.1583\ (\ln \text{LJFL});\ R^2 = 0.87 \quad (6)$$

females:

$$\ln W = -13.121 + 3.2734\ (\ln \text{LJFL});\ R^2 = 0.92. \quad (7)$$

Covariance analysis indicated that the slopes of length-weight regressions for male and female blue marlin in the common length range of 140–277 cm were significantly different (P 0.0001).

Growth

Observed and estimated length and weight-at-age are shown in Table 1, and all length-at-age data are shown

Table 2

Comparison of the precision of various ageing methods and structures for Atlantic blue marlin *Makaira nigricans*, bluefin tuna *Thunnus thynnus*, lemon shark *Negaprion brevirostris*, and little tunny *Euthynnus alletteratus* based on the average percent error approach of Beamish and Fournier (1981).

Species	Study	Age range (Ageing structure)	Units of ageing method	Average percent error Mean (Range)
Blue marlin	This study	0.024–1.4 years (otoliths)	days	1.6% (0.3–4.0%)
Bluefin tuna	Prince et al. (1985)	1–28 years (vertebrae)	years	none (0.3–6.3%)
Lemon shark	Brown (1988)	0.42–21 years (centrum)	months	3.4% (0–14%)
Blue marlin	McGowan et al. (1987)	2–10 years (spines)	years	none (0.02–0.09%)
Little tunny	Cayre and Diouf (1983)	1–8 years (spines)	years	10.5% (none)

in Figure 9 for males, females, and unknown sex combined. Length and weight-at-age, absolute growth rates (AGR, cm or kg/day), and relative growth rates (RGR, percent body length or weight/day) were computed for the first 495 days using the appropriate growth equation (Table 3). The maximum AGR for blue marlin (sexes combined, 1.66 cm/day) occurred at a length of 39 cm and an estimated age of about 50 days (Table 3). The AGR then decreased continuously to about 0.09 cm/day at 495 days. Relative growth rates decreased continuously from about 21% at 10 days to 0.04% at 495 days (Table 3).

The change in length-weight relationships which we detected at about 140 cm occurred later than the change in form of the length-at-age relationship (about 110 cm). Thus, our weight-at-age curves for fish >110 cm are composites derived from lengths of mostly immature fish (110–140 cm) where no differences in length-weight relationships were found, and adults where sexual dimorphism was evident. As a result, they show a small difference in growth rates for young males and females in the length range 110–140 cm, even though the data in this range do not indicate significant differences in either length-at-age or the length-weight relationship.

Our results show a slight decrease and then increase in AGRs for weight from 80 to 150 days, but this is probably an artifact of the estimation procedure. Parameter estimates are very highly correlated, indicating that growth in weight is essentially linear beyond the maximum relative growth rate for weight which occurs at about 70 days.

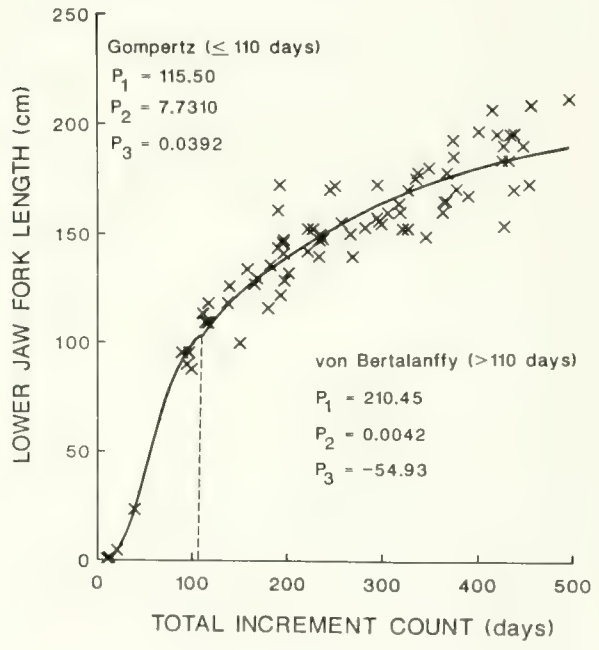


Figure 9

Length-at-age data fitted to the Gompertz equation (to the left of the vertical line) for the first 100 days of life (24 larvae and juvenile Atlantic blue marlin *Makaira nigricans*). Parameters (P_1, P_2, and P_3) are given; $R^2 = 0.98$. Length-at-age data fitted to the von Bertalanffy equation (to the right of the dashed vertical line) for the age range 110–495 days (71 young adult/adult blue marlin). Parameters (P_1, P_2, and P_3) are given; $R^2 = 0.77$.

Table 3

Growth of Atlantic blue marlin *Makaira nigricans* predicted by the Gompertz and von Bertalanffy equations[1] based on analysis of otoliths for the first 495 days of life. Estimated lower jaw fork length (LJFL, cm) are given for ages 10–495 days for all sexes combined, as well as estimated weights (kg) for males and females. Absolute growth rates (AGR) are given in cm or kg per day, and relative growth rates (RGR) are calculated as 100*AGR divided by length or weight.

	All sexes combined			Males only[2]			Females only[2]		
Estimated age (days)	LJFL length (cm)	AGR	RGR	Weight (kg)	AGR	RGR	Weight (kg)	AGR	RGR
10	0.62	0.13	20.49	0.00	0.00	0.00	0.00	0.00	0.00
15	1.58	0.27	16.84	0.00	0.00	0.00	0.00	0.00	0.00
20	3.39	0.47	13.84	0.00	0.00	0.00	0.00	0.00	0.00
25	6.36	0.72	11.37	0.00	0.00	0.01	0.00	0.00	0.01
30	10.66	1.00	9.35	0.01	0.00	0.02	0.01	0.00	0.02
35	16.30	1.25	7.68	0.03	0.01	0.04	0.03	0.01	0.04
40	23.10	1.46	6.31	0.08	0.02	0.06	0.08	0.02	0.06
45	30.77	1.60	5.19	0.18	0.03	0.09	0.18	0.03	0.09
50	38.95	1.66	4.27	0.37	0.05	0.12	0.37	0.05	0.12
55	47.27	1.66	3.51	0.66	0.07	0.15	0.66	0.07	0.15
60	55.42	1.60	2.88	1.07	0.09	0.17	1.07	0.09	0.17
65	63.17	1.50	2.37	1.58	0.11	0.18	1.58	0.11	0.18
70	70.34	1.37	1.95	2.17	0.13	0.18	2.17	0.13	0.18
75	76.84	1.23	1.60	2.83	0.14	0.18	2.83	0.14	0.17
80	82.62	1.09	1.31	3.52	0.14	0.17	3.52	0.14	0.17
85	87.70	0.95	1.08	4.20	0.14	0.16	4.20	0.14	0.16
90	92.11	0.82	0.89	4.87	0.13	0.14	4.87	0.13	0.14
95	95.90	0.70	0.73	5.49	0.12	0.13	5.49	0.12	0.13
100	99.13	0.60	0.60	6.06	0.11	0.11	6.06	0.11	0.11
105	101.87	0.50	0.49	6.58	0.10	0.10	6.58	0.10	0.10
110	104.17	0.42	0.41	7.04	0.10	0.09	7.04	0.10	0.09
115	106.11	0.44	0.42	8.88	0.08	0.08	9.77	0.09	0.08
120	107.72	0.44	0.41	9.18	0.08	0.08	10.09	0.09	0.08
135	116.59	0.40	0.34	11.04	0.09	0.09	12.06	0.10	0.08
150	122.39	0.37	0.31	12.48	0.10	0.08	13.60	0.11	0.09
165	127.83	0.35	0.28	14.01	0.11	0.08	15.25	0.11	0.09
180	132.93	0.33	0.25	15.64	0.11	0.08	17.01	0.12	0.09
195	137.72	0.31	0.23	17.36	0.12	0.09	18.88	0.13	0.09
210	142.21	0.29	0.20	19.17	0.12	0.09	20.87	0.14	0.10
225	146.43	0.27	0.19	21.05	0.13	0.09	22.96	0.14	0.10
240	150.39	0.26	0.17	23.01	0.13	0.09	25.15	0.15	0.10
255	154.10	0.24	0.16	25.04	0.14	0.09	27.44	0.16	0.10
270	157.58	0.23	0.14	27.12	0.14	0.09	29.83	0.16	0.10
285	160.84	0.21	0.13	29.27	0.14	0.09	32.30	0.17	0.10
300	163.91	0.20	0.12	31.45	0.15	0.09	34.85	0.17	0.11
315	166.78	0.19	0.11	33.67	0.15	0.09	37.48	0.18	0.11
330	169.48	0.17	0.10	35.93	0.15	0.09	40.18	0.18	0.11
345	172.01	0.16	0.10	38.21	0.15	0.09	42.94	0.19	0.11
360	174.39	0.15	0.09	40.50	0.15	0.09	45.76	0.19	0.11
375	176.62	0.14	0.08	42.80	0.15	0.09	48.62	0.19	0.11
405	180.67	0.13	0.07	47.41	0.15	0.09	54.46	0.20	0.11
435	184.23	0.11	0.06	51.97	0.15	0.08	60.40	0.20	0.11
465	187.37	0.10	0.05	56.45	0.15	0.08	66.39	0.20	0.11
495	190.14	0.09	0.05	60.81	0.14	0.08	72.38	0.20	0.11

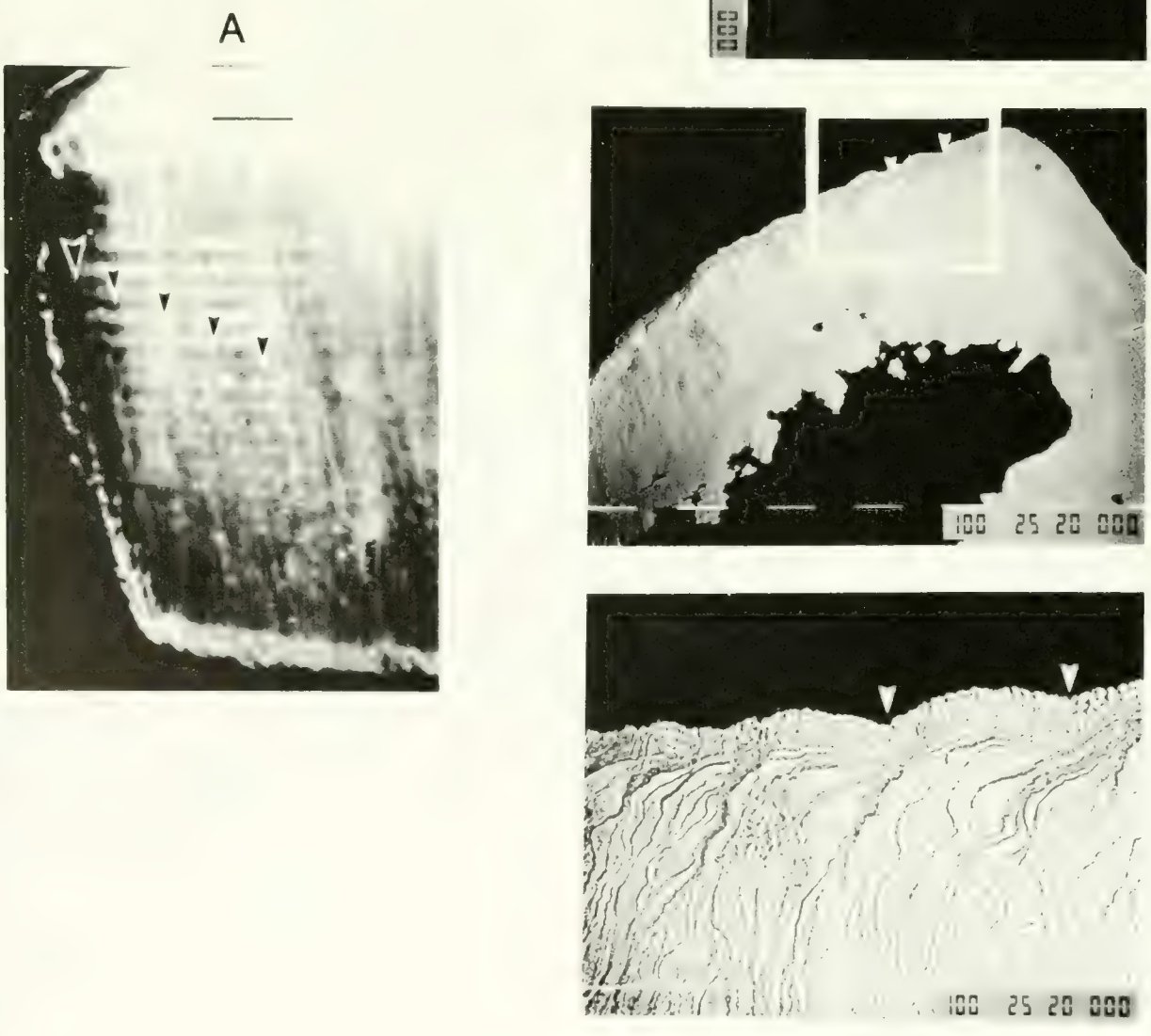
[1]Parameter estimates are shown below. Definitions for P_1, P_2, and P_3 are given in text.

Variable	Age interval	Equation	P_1	P_2	P_3
Length	<110 days	Gompertz	115.506	7.731	0.039
Length	>110 days	Bertalanffy	210.453	0.004	−54.933
Weight	<110 days	Gompertz	9.581	23.132	0.039
Weight (M)	>110 days	Gompertz	118.428	3.820	0.004
Weight (F)	>110 days	Gompertz	179.862	4.064	0.003

[2]The AGR and RGR for male and female weight are the same for 10 to 110 days.

Figure 10

(A) Photomicrograph of the video image of the whole otolith showing a medial view of the ventral lobe of a sagittae from a 258.0 cm LJFL male Atlantic blue marlin *Makaira nigricans*. White arrows show location of opaque zones of presumed annual increments. Black bar = 200 μm. (B) Scanning electron micrographs of the transverse section of the sagittae from a 140.5 cm LJFL male Atlantic blue marlin. White arrows on section (bottom) showing entire otolith and on the enlargements (middle and bottom) indicate approximate location of presumed annual zones identified in photomicrograph. White bars represent 1000 μm, 100 μm, and 100 μm from top to bottom, respectively.



Discussion

Limitation of the ageing method

Within the age range of 9 to 495 days, reliability of the ageing method decreased progressively with increasing age. An upper limit for optical resolution of primary increments occurred at a body length of about 212 cm. Beyond this length, depositions of individual increments were too close together to distinguish, and we did not feel that accurate counts could be made. Therefore, based on otolith appearance and increment spacing at the margin, we did not apply the otolith microstructure method to fish larger than 212 cm. While this limit is arbitrary and perhaps conservative, the practical application of this technique for Atlantic blue marlin will certainly be restricted to no more than the first 2 years of life.

Because of the morphology of blue marlin otoliths, the SEM technique is only practical for transverse sections. Although the microstructural record could sometimes be read for several hundred days longer than with a light microscope preparation, other limitations, such as irregularity in the ventral lobe, made this a difficult and impractical approach (see Fig. 10). The dorsal lobe has a very regular and easily read early-growth record (up to about 1.4 years), but has a very uneven margin. Incremental growth is greatly compressed and probably interrupted to varying degrees, depending on which particular radius is intersected by the section. Furthermore, the extremely small size of blue marlin otoliths (i.e., a maximum dorsal lobe radius of about 2 mm), combined with a probable maximum age exceeding 25 years (Hill et al. 1989), means that increments will average about 0.2 μm if a complete record is present. Counting such fine increments requires optimal sectioning, polishing, and etching and an otolith crystalline structure that will allow such fine structures to be seen. Increments of this width have been reported (Radtke 1984, Brothers and Mathews 1986); however, it is not clear whether such fine increments can always be seen.

The problem of increment resolution in larger/older blue marlin may have resulted in an underestimate of age and overestimated growth rate. Campana and Neilson (1985) state that apparent non-daily increment formation reported for some species (Geffen 1982) could be due to limited instrument resolution, as well as variable otolith preparation and retarded growth due to environmental conditions during deposition. We minimized these potential effects by rejecting hard-to-analyze samples and by using increment counts on lateral or sagittal views instead of transverse sections. The SEM examination of sagittal and transverse sections also helped confirm that errors of underestimating increments were minimized using the light microscope counting procedure. In addition, the chi-square contingency table analyses confirmed that significant errors in undercounting increments did not occur, assuming that the qualitative description of spawning in the literature is accurate.

Under optimal conditions, increments separated by less than 0.2 μm cannot be resolved with the light microscope. In practice, our observation is that with moderately thick sections and the complex three-dimensional morphology of istiophorid otoliths, the resolution limit is two or three times this value. Thus, otolith growth zonations narrower than about 0.5 μm will be underrepresented in the increment count. Since all increments in blue marlin sagittae were much larger than 0.5 μm (for fish $\leq$ 1.4 years of age), we feel this problem did not affect the results of this study. Although subdaily increments were commonly observed (Fig. 2), these features were easily distinguished from the primary increments (Figs. 2, 3) and thus overestimation of total increment count was probably not a source of error in this study.

Periodicity of increment formation

Back-calculation of spawning dates and descriptions of otolith microstructure are inherently less desirable for determining the periodicity of increment formation than direct approaches such as rearing fish of known age in captivity or chemical labeling (e.g., oxytetracycline, Geffen 1987). Geffen (1987) reviewed seven methods of age validation and rated each method according to levels of reliability for providing evidence of daily ring deposition. The otolith microstructure approach was characterized as providing a medium level of reliability, allowing only limited inferences for validation of daily ring deposition. Conversely, Geffen (1987) rated the estimation of hatching dates as a medium-to-highly-reliable method for evaluating the strength of assuming daily ring formation in teleost otoliths. Therefore, the results of our study should be tempered accordingly.

Otolith microstructure Our examination of microstructural features of blue marlin otoliths identifies and characterizes the primordium, core, primary increments, subdaily increments, and increment spacing. These microstructural features in larval blue marlin sagittae were indistinguishable from the same characteristics described in the sagittae of related teleost species, some of which had definitive age validation based on rearing experiments.

Back-calculated spawning dates There are several potential sources of error in the back-calculated spawning dates reported in this study. Since istiophorids have never been reared in captivity, we had no basis for correcting for the time of initial growth-increment formation in blue marlin sagittae. However, increment deposition has generally been reported to start within the first week after hatching in most teleosts, and in the majority of studies the first ring usually forms during the first 3 days after hatching (Brothers 1979, Brothers et al. 1983, Radtke 1983b). Therefore, this type of error probably did not bias our estimates of spawning dates by more than 7 days. In addition, we feel that the precautions taken to minimize underestimates of increment counts (discussed earlier) avoided major errors of this type.

Mahon and Mahon (1986) summarized existing data on spawning of blue marlin in the northwestern Atlantic (Erdman 1968, Eschmeyer and Bullis 1968, Yeo 1978) and reported that the spawning season occurs from April through November. Peak spawning is thought to occur primarily in midsummer (Erdman 1968), but a smaller peak in the fall has also been reported (Yeo 1978).

Our data on back-calculated spawning dates (Fig. 5A) agree with the qualitative data on spawning season reported by Mahon and Mahon (1986) and the peaks of spawning documented by Erdman (1968) and Yeo (1978). Back-calculated spawning dates are based on a wide range of fish age and dates of capture (Fig. 5B). As shown in Figure 6, periodicities other than 1 allocate substantial numbers of back-calculated spawning dates and peak spawning to months outside the reported spawning season. The results of the chi-square contingency table analyses and the observations of otolith microstructure are both consistent with the hypothesis that the increments in sagittae from young Atlantic blue marlin are formed once each day.

Precision

Blue marlin are considered to be a long-lived species (Hill et al. 1989) and thus potentially have many age-classes in the fishery. The APE method of evaluating the precision of a set of age determinations, described by Beamish and Fournier (1981), is not independent of age and thus appeared well-suited for blue marlin. Mean APE values (ranging from 0.3 to 4.0%) for blue marlin, in the age range 21–495 days, are well within the range published for other species (Table 2) using annual or monthly ageing methods. The APE values for these ageing techniques are not directly comparable to daily ageing methods (i.e., errors in daily increment methods obviously have a smaller effect on age estimation than errors from annual ageing methods). Nevertheless, the overall mean APE, 1.6% (as well as the range in APE values), indicates that the otolith microstructure method applied to young blue marlin clearly meets the requirement (<10%) described by Powers (1983) for an acceptable level of precision for use of an ageing technique in stock assessment.

Growth

The maximum absolute growth in length (1.66 cm/day at 39 cm LJFL) we report for young Atlantic blue marlin exceeds that estimated from length frequencies by de Sylva (1957) for Atlantic sailfish *Istiophorus platypterus* for the second month of life (1.10 cm/day for the length range 18–51 cm total length). De Sylva (1957) estimates that 6-month-old (180-day) sailfish attain a modal total length of 142.2 cm (~113.9 cm LJFL), while we found that blue marlin reach the same size in about 130 days. Also, while blue marlin and sailfish are almost the same size at the end of the first month, our average relative growth rate (5.7%) computed for the same size range as sailfish (RGR = 3.9%, 18–51 cm total length or about 10–38 cm LJFL) is nearly 1.5 times larger during the second month.

Growth rates are very rarely constant for extended periods of time during early life cycles, i.e., periods of rapid growth are usually followed by periods of declining growth giving rise to the S-shaped or asymptotic growth curves. Thus, it is almost certain that growth rates exceed the first 100-day average of 1 cm per day somewhere during this period. Both the magnitude and location of the estimated maximum depend to some extent upon the validity of the choice of the growth equation.

Our data suggest that blue marlin is one of the most rapidly growing teleosts in terms of absolute growth rates, but that larval, juvenile, and young adult/adult growth are not particularly exceptional measured on a relative scale. For example, maximum growth of the common dolphin *Coryphaena hippurus* does not exceed 0.5 cm/day for the first year of life (Pew 1957; C. Brownell, The Oceanic Inst., P.O. Box 25280, Honolulu, HI 96825, pers. commun., 6 Sept. 1988), but the species attains a maximum length of 1.5 m, compared with 4.5 m for blue marlin, one of the largest North Atlantic teleosts (Norman and Fraser 1948). Conversely, Atlantic bluefin tuna attain a maximum weight similar to Atlantic blue marlin (over 454.5 kg), yet the maximum growth rate of bluefin tuna for the first year is similar to dolphin and varies from 0.1 to 0.6 cm/day (Brothers et al. 1983). Similarly, as shown in Table 3, the relative growth rate (17%) for 1.5-cm LJFL blue marlin postlarvae is only slightly above that (13%) reported by Hunter and Kimbrell (1980) for Pacific mackerel *Scomber japonicus* postlarvae averaging 1.5 cm SL.

Interspecific comparisons of linear growth rates can be misleading if differences in body shape and resultant patterns of growth in body weight are not considered. Juvenile blue marlin are very elongate fishes, and the very high rates of growth in length correspond to only moderate rates of increase in weight. For example, the maximum calculated relative growth rate is 1.8% body weight per day at an age of about 70 days. This value is well within the typical range exhibited by teleosts (Weatherley 1972). Extraordinary consumption rates or conversion efficiencies would not be required to support the growth rates predicted in this study. Furthermore, since swimming speed usually increases with body length, this early growth period no doubt is advantageous for survival and sets the stage for the fast-swimming and wide-ranging capabilities of adults.

While sexual dimorphism in linear growth was not evident from our samples (perhaps due to small sample size), significant differences in the length-weight relationships were found above 140 cm. Our weight-at-age equations indicate small differences in growth rates between sexes for both length and weight may begin at about 110–120 cm.

Ageing adults

In order to evaluate the usefulness of the ageing methods used in this study on adult blue marlin (213–367 cm LJFL), SEM and light microscope analysis of the microstructural increments between presumed annual marks were examined on whole otoliths and transverse sections of 23 fish. Although the presumed annual marks (as described by Wilson 1984) were clearly visible in both the dorsal and ventral lobes of sagittae in adult fish over 300 cm LJFL (Fig. 10), the microstructural increments between these marks could not be clearly distinguished for accurate counts. Conversely, the presumed annual marks could not be distinguished on sagittae from the largest young adults (200–212 cm LJFL) while the microstructural increments were still visible. Therefore, this approach could not offer conclusive evidence for validating either daily or annual periodicities in blue marlin otolith deposition.

Incidental observations of relative otolith size (dimension and mass) in Atlantic and Pacific blue marlin indicate that individuals with relatively larger otoliths also have many more presumptive annuli in their otoliths compared with similar-sized fish (Wilson 1984, Hill et al. 1989). The coefficients of determination for linear regressions of these parameters are strong (range in R^2, 0.70–0.91; Wilson 1984). Further exploration of the relationships between fish size, otolith size, and increment counts coupled with validated ages for younger fish could lead to more robust regression techniques (Boehlert 1985) to estimate the age of adult blue marlin.

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Estimates of Age and Growth of Ehu *Etelis carbunculus* in Four Regions of the Pacific from Density of Daily Increments in Otoliths

M. Kimberly Smith

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole Street, Honolulu, Hawaii 96822-2396
Present address: State of Hawaii, Department of Land & Natural Resources
Division of Aquatic Resources, 1151 Punchbowl St., Rm. 330, Honolulu, Hawaii 96813

Eric Kostlan

Department of Mathematics, University of Hawaii
Manoa Campus, Honolulu, Hawaii 96822

Abstract.–Growth of the deep slope snapper *Etelis carbunculus* was evaluated from the density of daily increments in sagittal otoliths collected from Hawaii, the Commonwealth of the Northern Marianas Islands (NMI), French Polynesia, and Vanuatu. The rate of otolith growth (μm/day) as a function of otolith radius was fit by regression to a modified Gompertz rate curve and the age of fish estimated by integrating the equation. There were slight regional differences between the estimated values of each of the three otolith growth rate parameters, which may be attributable in part to random sampling differences. However, integrated estimates of fish age versus otolith radius varied little between sites because of the compensatory relationship between two of the three estimated parameters which together determine the rate of dampening of the otolith growth function. There were significant regional differences in average otolith radius, and thus in estimated age, as a function of fish length. Fish from Vanuatu and NMI were younger at a given length than those from the other two regions. However, fish as large as those at Vanuatu are not found at NMI, suggesting there may be regional differences in mortality. Regional age-at-length data were fit to a von Bertalanffy growth curve, both unconstrained and held to a value of asymptotic length (L_∞) obtained from the literature. Estimates of natural mortality for each region are discussed, based on the regional values obtained for the von Bertalanffy growth constant (K). These results should be confirmed using data obtained from a wider range of fish sizes.

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The observation of microscopic markings in thin sections of the otoliths of fishes, with evidence that these marks present a record of daily growth (Panella 1971, 1974), provided an alternative means of ageing tropical species for which seasonal and annual growth rings are often hard to interpret. These marks are produced in many fishes (Brothers et al. 1976, Struhsaker and Uchiyama 1976, Wild and Foreman 1980, Neilson et al. 1985, Jones and Brothers 1987, and others). Counting otolith microincrements has proved useful in estimating the growth of juvenile and larval fishes (Barkman 1978, Methot 1981, McGurk 1984, Jones 1986, Geffen 1986), because they have small and transparent otoliths with readily interpretable microincrements. While offering the opportunity to detect growth on a more sensitive scale, the laborious process of enumerating all the daily increments in the otoliths of older organisms has limited the widespread use of this technique (Ralston and Williams 1988a).

From the late 1970s through the mid- and late 1980s, Ralston and colleagues (Ralston 1976, 1981, 1985; Ralston and Miyamoto 1981, 1983; Ralston and Williams 1988a) developed a labor-efficient method of estimating the age and growth rate of fishes using microincrement data from otoliths. This method, based on numerical integration of otolith growth rates from the density of presumptive daily increments, was applied by S. Ralston and H.A. Williams (Honolulu Lab., NMFS Southwest Fish. Sci. Cent., Honolulu, HI, unpubl. data) to a number of Pacific Ocean commercial species. It provided an estimate of the von Bertalanffy (1957) growth curve for which the asymptotic length (L_∞), growth constant (K), and age at zero length (t_0) were within the range of previous regional estimates for many of the 24 species for which the method was tested.

However, three out of four growth curves estimated by this method for the deep slope "red" snapper *Etelis carbunculus* (known as ehu in Hawaii), did not reach an asymptotic length, instead having the form of a straight line with positive slope. These results were considered to be anomalous, since collections included fish at or near the regionally estimated values of asymptotic length (although the sample size for some regions was very small). Otolith collections for this species came from Hawaii, Vanuatu, French Polynesia, and the

Commonwealth of the Northern Marianas Islands (NMI). In the single case where the estimated von Bertalanffy growth curve did reach an asymptote (379 mm for NMI), it did so considerably below the maximum length commonly found in that region (580 mm) and well below the maximum length included in the data.

The present study reevaluated the method of age and growth estimation using the same data, in an attempt to see if growth estimates could be improved. In response to some of the problems encountered in reprocessing the data, the methodology of integrating and fitting was modified in a manner that may prove useful to other researchers. In addition, some important guidelines for collecting data for growth estimation from integrated microincrement densities were developed.

Methods

Ralston and Williams' otolith growth data (unpubl.) from Hawaii, Vanuatu, French Polynesia, and NMI were reevaluated, using a new method that employs both analytical and numerical integration of the rate curve. Fork lengths were recorded and sagittal otoliths removed from fish caught with bottom handlines at depths of 80–200 m in the four regions. The data were collected and compiled by Ralston and Williams from 1982 to 1988. They collected a wide size range of fish, but made no systematic sample of a representative number of organisms of each size. Small fish, not ordinarily captured with the large hooks used by commercial fishers, were underrepresented in all regional samples. Collections were essentially random, within the size range selected by this fishing gear. Since the principal objective was to find an appropriate method of fitting and integration, this limitation was acceptable.

Otoliths were prepared and microincrement densities on the postrostral axis recorded from video-relayed images using techniques described by Ralston and Williams (1988a). The data available for each fish included fork length, total otolith postrostral radius, and a series of estimates of microincrement density at various points along the otolith radius. Microincrement densities were registered in microns per increment, calculated by dividing the length of the radial segment by the number of increments counted within it. Following the assumption of Ralston and Williams (1988a) and Brouard et al. (1983) that microincrements are deposited on a daily basis for *Etelis carbunculus*, increment densities represent otolith growth rate (microns/day) as a function of distance from the origin of growth, or focus. Validation of daily increment deposition for most deep slope snappers has not been obtained because of low survival when fish are brought to the surface. However, validation was obtained for *Pristipomoides filamentosus* (Ralston 1981), another eteline snapper found in similar habitat and locations.

Ralston's method of age integration consists of estimating the time transpired within consecutive 500-μm intervals of otolith radius, by multiplying the length of each interval by its mean growth rate (microns/day). The estimated number of days required to grow through each 500-μm radial interval are then summed numerically, producing a series of estimated ages for fish with otoliths measuring 500, 1000, 1500 μm, etc. The relationship between the natural logarithms of fork length and otolith radius, determined by regression from each regional sample, is then used to estimate fish length at the midpoint of each 500-μm interval of otolith radius. The resultant age-at-length data are fit to a von Bertalanffy growth curve by nonlinear regression. In this way, estimated fork lengths for a hypothetical group of fish with otoliths measuring 250–9250 μm (by intervals of 500) are fit to age estimates for otoliths at 500–9500 μm (by 500-μm intervals). Actual fork lengths and otolith measurements are used only to estimate the relationship between fork length and otolith radius. In addition to the slight difference in otolith radius (250 μm) between age and length estimates, the validity of the assumption that the length of fish as a function of otolith radius can be accurately predicted from a regression curve obtained from the original sample depends on having had a representative size range and number of individuals from each population. Rather than incorporate this sampling error, it was decided to concentrate on using the otolith growth-rate data to obtain integrated age estimates for the fish and otoliths sampled.

Early attempts at integrating the otolith growth function were aimed at reducing the size of the radial interval used to approximate the growth rate. This was found to be impractical for various reasons. The average number of microincrement density estimates ("readings") per fish ranged from 4.1 to 61.5 regionally. Otoliths from Hawaii and French Polynesia were measured more extensively; 1681 and 3877 readings were made from 37 and 63 otoliths, respectively. For NMI and Vanuatu, fewer measurements were made (252 and 141 from 62 and 13 otoliths, respectively). Because of these differences in the number and distribution of microincrement density readings along the otolith radius, the reliability of mean otolith growth rates and resultant age estimates varied widely as a function of the length of the radial interval chosen. The asymmetry of the otolith growth-rate function compounded this problem. Therefore, an alternative method of integration that did not rely on mean microincrement densities as a function of radial intervals was chosen.

Estimates of otolith growth rate as a function of radius were fit by SAS (1985) nonlinear regression to a modified Gompertz rate curve (Gompertz 1825, Winsor 1932) of the form

$$y = axe^{-bx} + c \tag{1}$$

where y = estimated density of daily increments or otolith growth rate (μm/day),
x = radial distance (μm) at which each density was recorded,
a and b = shape parameters,
c = a constant representing the asymptotic otolith growth rate.

The Gompertz rate curve was chosen for its general shape and was then modified in form to provide a better fit to observed data. The constant was added because recorded microincrement densities did not subside to zero, instead reaching a low positive value.

Substituting dx/dt for y in equation (1) gives a clear picture of the otolith growth-rate function. Since the growth rate was estimated in days, the integral of the reciprocal of the righthand side of this function provides an estimate of the fish age in days as a function of otolith radius in microns, as follows:

Since $dx/dt = axe^{-bx} + c$

then
$$t_x = \int_m^n \frac{dx}{axe^{-bx} + c} \tag{2}$$

where m and n are any two distances along the otolith radius. Substituting $u = bx$ and $du = bdx$ gives

$$t_x = \int_{mb}^{nb} \frac{du/b}{(au/b)e^{-u} + c} \tag{3}$$

$$= \frac{1}{cb} \int_{mb}^{nb} \frac{du}{(a/bc)ue^{-u} + 1}$$

$$= \frac{1}{cb} \int_{mb}^{nb} \{\sum_{k=0}^{\infty} ((a/bc)ue^{-u})^k (-1)^k\}\, du$$

$$= \frac{1}{cb} \sum_{k=0}^{\infty} (-1)^k \int_{mb}^{nb} [(a^k/b^k c^k)\, u^k e^{-ku}]\, du$$

$$= \frac{n-m}{c} + \sum_{k=1}^{\infty} \frac{(-1)^k a^k}{b^k c^k k^{k+1}} \Gamma(k+1, kmb)$$

$$- \sum_{k=1}^{\infty} \frac{(-1)^k a^k}{b^k c^k k^{k+1}} \Gamma(k+1, knb) \tag{4}$$

where Γ is the incomplete gamma function and k is a dummy variable. The first term, representing the asymptotic growth rate, is solved separately. Using the ratio test for convergence and an estimate based on the Gaussian continued fraction

$$V^k e^{-V} < \Gamma(k+1, V) < \frac{(V^{k+1} e^{-V})}{V-k} \tag{5}$$

(in Wall 1948), the first series converges for $mb > M$ and the second for $nb > M$, where M is a solution of

$$\frac{M^2 e^{-M}}{M-1} = bc/va \quad \text{and v is any number } > 1. \tag{6}$$

Thus, for each set of values of a, b, and c, a distinct point can be identified at which the expanded series converges quickly. For speed of computation, we chose v = 2, to ensure that the ratio of consecutive integrals would be less than 1/2. Age in days was estimated for each otolith radius by a Fortran program, adapted from Davis and Rabinowitz's (1984) routine for Romberg integration. Given values of x (otolith radius in microns), a, b, and c, the program first solves equation (6) by Newton's method (in Atkinson 1989) and then either uses the expanded series from equation (4), if it converges quickly, or evaluates the integral given in equation (3) by Romberg integration. Both estimates were made with a tolerance of 10^{-15}.

Fork lengths and estimated ages of the fish sampled were fit to the von Bertalanffy (1957) growth curve

$$L_t = L_\infty (1 - e^{-K(t-t_0)}),$$

where L_∞ and t_0 represent theoretical values of asymptotic length at infinite age and age at zero length, respectively; K is a growth constant; and t is fish age in years. The Marquardt method of iterative least-squares fitting was used, under SAS (1985) nonlinear fitting procedure. For comparison, the data were also fit by von Bertalanffy's method of log-linear regression, using a BASIC program by Gaschütz et al. (1988).

Table 1

Summary of otolith collections and maximum size of red snapper *Etelis carbunculus* by region.

Collection site	No. of otolith	Fork lengths (mm)					
		Sampled				Recorded or estimated	
		Min.	Max.	Avg.	SD	MLR*	ML_∞**
Hawaii	37	226	641	428.2	101.6	700 (1)	718 (5)
Fr. Polynesia	63	160	510	351.5	82.0	680 (2)	—
No. Marianas	62	29	527	337.5	66.3	540 (3)	537 (6)
Vanuatu	13	270	920	520.8	194.4	1270 (4)	993 (7)

*MLR = Maximum length recorded (from regional fishery statistics).
**ML_∞ = Average of three estimates of asymptotic length (L_∞) for the von Bertalanffy growth curve (from the literature).

Sources of MLR estimates

(1) United Fishing Agency, Ltd. (UFA), Honolulu, pers. commun., July 1988.
(2) Wrobel 1985
(3) National Marine Fisheries Service (NMFS), 1982–84. RAIOMMA Cruise data, unpubl. logs, NMFS Honolulu Lab.
(4) R. Grandperrin, ORSTOM fisheries biologist, Mission ORSTOM, New Caledonia, pers. commun., Feb. 1989.

Sources of ML_∞ estimates

(5) Ralston and Kawamoto 1987, Uchida et al. 1982
(6) Ralston and Williams 1988b, NMFS RAIOMMA data 1982–84
(7) Brouard et al. 1983, Brouard and Grandperrin 1985, Carlot and Nguyen 1989

Table 2

Estimated otolith growth-rate parameters and summary statistics for the modified Gompertz rate curve by region for red snapper *Etelis carbunculus*.

Location		Parameter estimate	±95% CI	Asymptotic correlation matrix		
				a	b	c
Hawaii	a	0.0688	±0.00311	1	0.741	−0.038
	b	0.0018	0.00005	0.741	1	0.499
	c	2.4242	0.22536	−0.038	0.499	1
			*R^2 0.713, n 1680,	**RSS 14211		
French Polynesia	a	0.0991	0.00357	1	0.764	0.006
	b	0.0021	0.00004	0.764	1	0.474
	c	2.4086	0.17919	0.006	0.474	1
			R^2 0.647, n 3877,	RSS 58776		
Commonwealth Northern Marianas	a	0.1111	0.01365	1	0.881	0.335
	b	0.0021	0.00014	0.881	1	0.624
	c	2.2672	0.43602	0.335	0.624	1
			R^2 0.824, n 252,	RSS 1251		
Vanuatu	a	0.0702	0.01180	1	0.866	0.204
	b	0.0019	0.00017	0.866	1	0.502
	c	2.1076	0.41886	0.204	0.502	1
			R^2 0.801, n 141,	RSS 467		
Overall (all locations combined)	a	0.0884	0.00250	1	0.765	0.012
	b	0.0020	0.00003	0.765	1	0.489
	c	2.3961	±0.13758	0.012	0.489	1
			R^2 0.661, n 5941,	RSS 76799		

*Multiple correlation coefficient $R^2 = [\Sigma(\hat{Y}_i - \bar{Y})^2/\Sigma(Y_i - \bar{Y})^2]$
**RSS = Residual sum of squares

Results

Number of otoliths, fish size range, and locations of collections are summarized in Table 1. For comparison, the maximum length registered in fisheries landings (MLR) and mean of available estimates of asymptotic length (ML_∞) for each region and their sources are also included. Intermediate sizes were represented in the data from most regions, but extremely large or small fish were underrepresented or lacking. The sample from Vanuatu was very small, but encompassed a wider range of fish lengths than was sampled from any other location. The limitations of the data must be kept in mind in interpreting and comparing results.

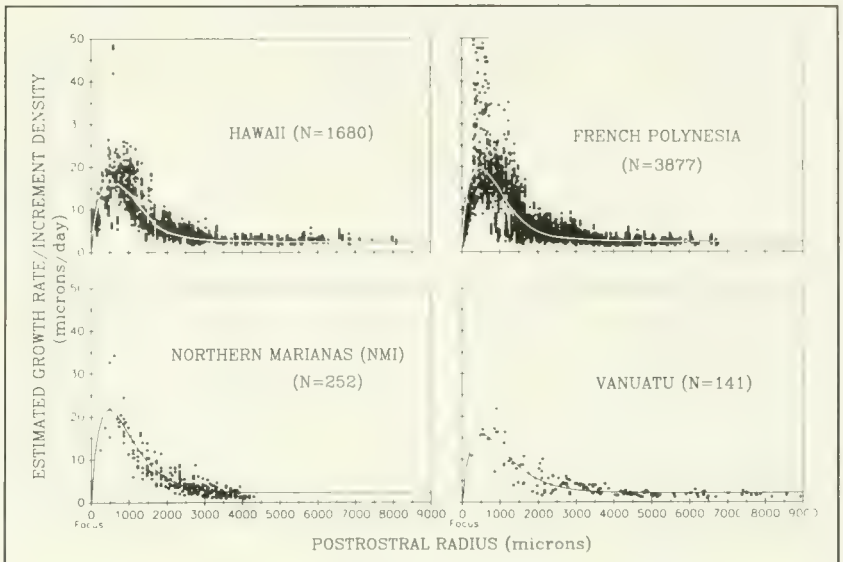

Figure 1
Estimated otolith growth rate and recorded microincrement densities for red snapper *Etelis carbunculus*.

Nonlinear regressions of otolith growth rate versus otolith radius in microns (Table 2) produced estimates of the parameters a, b, and c of the rate equation, with asymptotic 95% confidence intervals. Multiple correlation coefficients were calculated for each regression as an additional index of fit. Data were pooled for all locations to estimate a global rate for otolith growth. The multiple correlation coefficients are low for these curves, due to the wide range of variation in recorded increment density near the focus (high residual variance). Predicted curves and recorded microincrement densities for each region were compared (Fig. 1). The function chosen mimics the behavior of the rate curve fairly well; however, the fit could be improved in the descending portion of the curve between 500 and 1500 μm of otolith radius. Few readings were made close to the otolith focus (<246 μm) for NMI and Vanuatu samples (Fig. 1). Fitting the data to the rate curve assumes that these otoliths grew similarly to those for which the ascending portion of the curve was sampled. The fit for the descending portion of the curve is supportive of this assumption. However, since the widest range of variation in recorded microincrement densities was always found close to the focus, these results should be interpreted cautiously.

Predicted ages at equal otolith radius, using the parameters in Table 2, were calculated for each region (Table 3a). Although there were differences between the estimated regional otolith growth parameters, predicted ages as a function of otolith radius were generally similar. The relationship between the shape parameters a and b is such that differences between them can be compensatory, one (a) controlling the amplitude of the rate curve and the other (b) the rate of dampening. The radius at which peak otolith growth rate is estimated (the maximum of the otolith growth-rate function) was similar regardless of region or weighting. Peak growth rate occurs where the derivative of $axe^{-bx} + c$ is equal to zero, or at $x = 1/b$. Estimated ages for this radial distance are included in Table 3a, where it can be seen that the otoliths of ehu from all regions reach their maximal growth rate between 1 and 2 months of age. Otoliths reach a constant growth rate before fish are 1.5 years old, or between 3000 and 3500 μm of otolith radius.

For comparison, the age estimates made by Ralston and Williams for comparable 500-μm intervals of otolith radius are given in Table 3b. The values are similar in many respects for Hawaii and French Polynesia (where more microincrement density estimates were made), but there are observable differences for all regions. Ralston and Williams' age estimates were lower close to the otolith focus, the two estimates were equivalent at intermediate radius, and their estimates were again lower at greater otolith radius. The exception to this pattern was seen for Vanuatu, for which our estimates were substantially lower at maximum radius. The radius at which the two estimates were equivalent and the magnitude of the difference between them varies from one region to another and is a function of the amount and variability of microincrement density readings and their effects on both estimates. The best check of which method gave more accurate results would be

Table 3A

Predicted ages at equal radial distances from estimated otolith growth rates for the red snapper *Etelis carbunculus*. NMI = Northern Marianas.

Otolith radius (μm)	Estimated age (days)				
	Hawaii	F. Poly.	NMI	Vanuatu	Overall
10	3.2	3.1	3.2	3.5	3.1
100	20.0	16.9	16.4	21.0	17.9
500	50.2	40.7	38.5	51.8	43.6
1000	82.4	68.6	65.3	85.7	72.8
1200	98	83	80	102	88
1400	116	101	98	122	106
1600	137	123	120	146	128
1800	163	150	147	174	154
2000	193	182	181	208	186
2500	290	292	298	319	292
3000	423	441	457	472	437
3500	586	619	648	657	611
4000	769	813	855	865	804
4500	964	1015	1071	1084	1005
5000	1164	1220	1289	1309	1211
6000	1573	1634	1729	1766	1627
7000	1985	2049	2170	2225	2044
8000	2398	2464	2611	2684	2461
9000	2810	2879	3052	3144	2878
10000	3223	3294	3493	3603	3296
11000	3635	3710	3934	4063	3713
12000	4048	4125	4375	4523	4130
13000	4460	4540	4816	4982	4548
14000	4873	4955	5257	5442	4965
	Age at 1/b μm of otolith radius				
Age (days)	555.5	484.8	467.7	532.5	504.8
1/b	53.5	39.9	37.0	53.9	43.8

Table 3B

Ralston and Williams' age estimates at equal otolith radius for the red snapper *Etelis carbunculus*.

Otolith radius (μm)	Estimated age (days)			
	Hawaii	F. Poly.	NMI	Vanuatu
500	46.7	40.7	25.1	37.5
1000	76.7	68.2	51.6	69.3
2000	193	191	172	211
2500	289	295	272	311
3000	422	416	418	433
3500	570	568	622	580
4000	758	764	866	759
4500	937	960	1250	1006
5000	1119	1157		1276
6000	1479	1571		1937
7000	1795	1955		2663
8000	2158			3181
9000				3997

to count all microincrements to a specific radius for the same otoliths. This was beyond the scope of the present study.

Fork lengths and age estimates, obtained by integrating the rate curve over the corresponding otolith radius (Appendix 1), were fit to a von Bertalanffy growth curve (Table 4). Both unconstrained regression and regressions with constraints on asymptotic length (L_∞) or age at zero length ($t_0 = 0$) were tested. Regressions with the highest indices of correlation were generally obtained by forcing the curve through an estimate of asymptotic length obtained from the literature or from regional fisheries statistics. The greatest value of MLR or ML_∞ from Table 1 for each region was used as an approximation of an appropriate forcing value. The criterion for convergence was based on a minimum level of improvement in the ratio of subsequent sum of squares errors (SSE):

$$(SSE_i - SSE_{i-1})/(SSE_i + 10^{-6}) < 10^{-8}.$$

Regressions which didn't converge after 200 iterations were eliminated. NMI was the only region for which the regression was able to converge with the constraint that $t_0 = 0$. Two fish from French Polynesia were omitted from the data, because their otolith radial lengths were not recorded.

Log-linear regressions using the Gaschütz et al. (1988) BASIC program were also done for comparison. These are weighted regressions of average age-at-length for NMI and French Polynesia, which had more than 50 observations. Figure 2 shows the best four growth curves (from Table 4). For all regions except NMI, these were the nonlinear regressions constrained in L_∞. The nonlinear method of fitting was preferred because it involved no artificial reduction of the variance observed in the data. For NMI the nonlinear regression constrained only to $t_0 = 0$ was used, because it had a higher r^2 value and lower residual variance. None of the curves for NMI showed a good fit; these results are included for comparison.

The scatterplot of age-at-length data (Fig. 2) illustrates the limitation on regression estimates imposed by the size range and number of fish sampled for each region. The most significant constraints on fitting a growth curve to the data were the high variance of estimated age (otolith radius) as a function of fork length, particularly for NMI and French Polynesia, and the limited range of fish sizes sampled. It was necessary to constrain most of the growth curves to an independently estimated value of L_∞, since there were few data points to represent extremely large or small fish. Although unconstrained curves could be fit to the

data for Hawaii and French Polynesia, these reached values of L_∞ far above lengths of fish captured in these regions throughout the history of their fisheries. For NMI and Vanuatu, nonlinear regressions tended towards unlimited L_∞. These results were similar to those of Ralston and Williams, indicating that the primary limitation on accurate growth estimation was probably the range of fish lengths sampled.

However, the present regressions differ from those of Ralston and Williams' in that they are derived from age estimates for measured otoliths and fork lengths, rather than from estimated lengths at equally spaced intervals along the otolith radius. Ralston's method produces an artificially broader and more uniform sample. This is evident in that the one region (NMI) for which the previous estimate was able to converge showed an inadequate fit by the present method, which is consistent with the clustering of data points in the middle of the size range (Fig. 2). Experimental fitting to a Gompertz curve was done initially, but it was found that lack of fit by either method was more attributable to the variance in age estimates and the narrow range of fish sizes than to the choice of a growth curve. The regression of otolith radius on fork length was allometric for all regions examined, so it is not surprising that somatic growth rate is represented as well by the von Bertalanffy curve.

The von Bertalanffy growth constant (K) for the best curves for each region were in the range of 0.129–0.137 for Vanuatu, 0.179–0.310 for NMI, 0.064–0.190 for Hawaii, and 0.039–0.145 for French Polynesia. The highest value of K = 0.464 for NMI, estimated by log-linear regression, was arbitrarily left out of the range for this region as being abnormally high. Any of the estimates for NMI could well be excluded on the basis of the r^2 values. Estimates of natural mortality (M) for these K values using the relationship for snappers and groupers by Ralston (1987) and for various taxa by Ricker (1973) are listed in Table 5. These K estimates agree with those summarized by Manooch (1987) for other species of lutjanids, including several of the subfamily etelinae.

Table 4

Summary of estimated growth by region for the red snapper *Etelis carbunculus*.

Region/Fitting assumptions	L_∞ (mm)	t_0 (yr)	K	R^2	RSS*
Hawaii (*N* 37)					
von Bertalanffy (unconstrained)	1182.8	2.06	0.064	0.920	30507
von Bertalanffy fix L_∞ = 718 mm	718.0	3.32	0.163	0.874	35005
von Bertalanffy fix L_∞ = 718 (linear**)	718.0	4.03	0.190	0.884	44250
Vanuatu (*N* 13)					
von Bertalanffy (unconstrained)	(no convergence)				
von Bertalanffy fix L_∞ = 1270 mm	1270.0	1.41	0.129	0.911	37503
von Bertalanffy fix L_∞ = 1270 (linear)	1270.0	1.62	0.137	0.920	39095
French Polynesia (*N* 60)					
von Bertalanffy (unconstrained)	1458.6	1.13	0.039	0.784	86365
von Bertalanffy fix L_∞ = 680 mm	680.0	2.35	0.126	0.756	89370
von Bertalanffy fix L_∞ = 680 (linear)	680.0	3.05	0.145	0.837	65115
Northern Marianas (*N* 62)					
von Bertalanffy (unconstrained)	(no convergence)				
von Bertalanffy (linear/unconstrained)	750.0	−0.18	0.179	0.576	115656
von Bertalanffy fix L_∞ = 540 mm	540.0	−0.23	0.289	0.435	142350
von Bertalanffy fix L_∞ = 540 (linear)	540.0	0.94	0.464	0.519	130986
von Bertalanffy fix L_∞ = 540, t_0 = 0	540.0	0.00	0.310	0.504	143137
von Bertalanffy fix t_0 = 0 (only)	583.2	0.00	0.273	0.572	142493

*RSS = Residual sum of squares.
**Linear = Log-linear regression and linear correlation coefficients from Gaschütz et al. (1988) BASIC program.

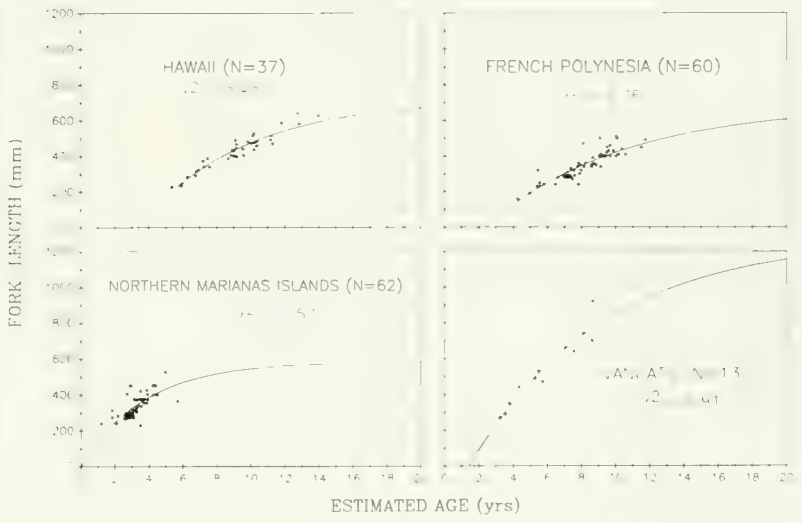

Figure 2

Estimated regional von Bertalanffy growth curves for red snapper *Etelis carbunculus*.

Table 5

Best estimated von Bertalanffy growth constant (K) and corresponding natural mortality estimates by region for the red snapper *Etelis carbunculus*.

	Range of best K estimates	Estimated natural mortality (M)	
		Ralston (1987)*	Ricker (1973)*
Hawaii	0.064–0.190	0.301–0.410	0.279–0.412
Vanuatu	0.129–0.137	0.285–0.301	0.258–0.279
French Polynesia	0.039–0.145	0.099–0.318	0.032–0.299
Northern Marianas	0.179–0.310	0.388–0.658	0.384–0.715

* Sources of regressions used to estimate natural mortality rate (M) from the value of the von Bertalanffy growth constant (K).

Discussion

The method presented is a variation on previous techniques of obtaining age estimates from microincrement densities (Methot 1983, Ralston and Williams 1988a, Gauldie et al. 1989). It provides a direct estimate of the fit of the rate function used to approximate the otolith growth curve, which is then integrated essentially without error. Part of the difficulty in comparing the present age estimates with those of Ralston and Williams was that a direct measure of error was not available for their estimates. Within the constraints of the fit of each rate curve, the present technique provides an accurate estimate of age at any chosen interval of otolith radius. The method also allows age estimation from the otolith focus to its perimeter, where readings become difficult, and gives a reliable estimate of the time transpired between any two points on the otolith radius.

The error introduced in numerical integration by the trapezoid method, dividing the otolith radius into increments of equal length and using the mean growth rate in each interval to estimate age, is well understood (Salas et al. 1986, Atkinson 1989). Most alternative methods of numerical integration have been developed to reduce the error introduced by the trapezoid estimate. Romberg's method is one of the most effective ways of eliminating this error, evaluating and subtracting it out as part of the process of integration. The result is a negligible integration error for the purposes of this discussion. The error in the present method derives from natural variability in otolith growth rates, lack of fit of the chosen rate curve, and any inadequacies in the data. The first two sources of error are measured by the sums of squares, and are represented in the multiple correlation coefficient and asymptotic confidence intervals for parameter estimates. Thus, another advantage of the present method is that alternative curves can be fit to evaluate the advisability of using other functions or combinations of functions to fit the data.

The reliability of these growth estimates is dependent, among other things, upon the assumption that Ralston and Williams were able to count all or most of the increments present in the otoliths at a given radius. This is true to a varying extent; however, the reliability of the readings may decrease as fish get older. Most microincrement density measurements were made within 50–60% of the total otolith radius. However, in each region, there were "legible" segments near the perimeter of some otoliths. The sectioning techniques and optical resolution of the Nikon light microscope and RCA video system used to observe the slides were sufficient to see detail considerably below the scale on which microincrements were recorded. Therefore, we believe that any error in the data is unlikely to have been derived from a failure to observe increments that were present.

Some error in measuring total otolith radius may have occurred, however, due to changes in the orientation of growth along the postrostral axis as fish get larger. Difficulties in reading otolith microincrements in older fish, induced by the transformation in shape and crystalline structure of the otolith affect the legibility of daily increments (Radtke 1987, Davies et al. 1988). Thus an important follow-up to these preliminary estimates is to confirm the orientation of the postrostral growth axis as a function of otolith size for each region. The hypothesis that otolith growth rate is essentially constant beyond a certain radius could be tested by reexamining microincrement densities for some of the larger otoliths near their perimeter.

A difference in actual microincrement densities at maximum otolith radius would influence age estimates significantly. An unmodified Gompertz rate curve (without the constant) was used in early attempts at fitting microincrement densities. This curve fit the data fairly well for small otolith radius, but the decline of the rate curve to zero at greater radius provided a poor fit and caused age estimates for large fish to increase by more than an order of magnitude. A constant was added to the rate curve for these reasons, significantly improving the fit and bringing age estimates into conformity with other estimates by fishery biologists and experienced fishers.

The growth estimates presented can be improved by sampling a wider size range and larger number of organisms and by recording microincrement densities

along the full length of the radial axis of all otoliths sampled. For very small fish, increments near the focus can be counted and integration is not necessary to get an age estimate. The size of the sample would be determined by the variance of otolith radius as a function of fork length, a characteristic which varies regionally. Otolith radius, and thus estimated age, was highly variable for a given fork length for all regions for which a sufficiently large sample was available to make this determination. This is evidence that a fairly large sample is necessary in order to have a reliable growth estimate. Sampling a representative number of fish within a full range of sizes and obtaining increment density measurements along the entire otolith radius are important, and should not be done at random.

Despite the utility of the technique of age estimation developed, potential biases in size range and number of otoliths sampled make it difficult to compare growth estimates for *Etelis carbunculus* quantitatively. Results presented imply that a more systematic sampling program may document significant regional differences in growth and population dynamics of this species. The relationship between otolith growth rate and postrostral radius was similar for all regions. However, there were regional differences in the width of otoliths for a given fork length (Appendix 1), wider otoliths being found in Hawaii and French Polynesia. Although there were few fish sampled from Vanuatu and limited overlap occurs with small organisms from the other regions, fish from NMI and Vanuatu had smaller otolith radius (lower estimated age) than fish of similar size from the other two areas. This means that even if growth rates of otoliths were essentially equal throughout the Pacific, fish would be older at a given fork length in Hawaii and French Polynesia. Thus, well below the forced values of asymptotic length used in regressions, regional differences in estimated age are apparent.

Fish apparently grow faster at Vanuatu and NMI than in any of the other regions. However, at NMI they reach less than half the size found in the region near Vanuatu. This suggests there are differences in natural mortality rates for these regions (asymptotic length estimates were obtained from virgin stocks for NMI and in the initial stage of the fishery at Vanuatu). The growth curves for NMI yielded higher estimates of the von Bertalanffy growth constant (K) and, as a result, natural mortality estimates were higher. The differences in K hold true even for the NMI regression that was constrained only in t_0, but as mentioned the results from NMI should be interpreted with caution. Hawaii and French Polynesia showed similar values of K to Vanuatu, but fish from these regions had thicker otoliths and were apparently more slow growing. Possible explanations for such differences include genetic differences in regional stocks, variation in the mean annual temperature, and differences in feeding or food availability.

The estimates of the von Bertalanffy growth curve were in the range of those obtained in previous studies. Although Uchida et al. (1982) estimated K at 0.36 for the Hawaiian Islands, Ralston and Kawamoto (1987) obtained values of 0.15–0.17, which is more consistent with the present results. Both Uchida et al. (1982) and Ralston and Kawamoto (1987) based their estimates on length-frequency data from exploited stocks. Ralston and Williams (1988b) estimated K for virgin stocks at NMI from 0.13 to 0.35, depending on the method used. K estimates from commercial landings data at the onset of the fishery at Vanuatu were in the range 0.07–0.19 (Brouard et al. 1983, Brouard and Grandperrin 1985). Thus, the present K estimates seem reasonable. Estimates of t_0 were considerably greater than zero, except in the case of NMI, which was almost certainly a function of the limited number of small fish included in the data.

The similarity of otolith growth rate at any given radial distance was pointed out by Ralston and Miyamoto (1983), but these authors did not discuss the implications with regard to otolith shape for fish with different growth rates. The similarity of growth rate of otoliths and regional variation in growth rate of fish may explain some regional differences in otolith shape. It also indicates that there are species-specific characteristics of otolith growth from one region to another, as would be expected. If the concept of narrower or thinner otoliths corresponding to faster-growing organisms within a given species can be generally applied to fishes, then this is a tool that can be useful for a number of purposes (for example, in evaluating paleontological evidence of growth rates in sedimentary strata). Although environmental and genetic components of otolith shape must also be considered, differences in growth rate may explain many of the differences in shape which have commonly been used to separate the otoliths of different stocks, or "races," of the same species (Postuma and Zijlstra 1958, Parrish and Sharman 1959, Kotthaus 1961, Messieh 1972, Bird et al. 1986). Variation in growth may also explain sex-linked differences in the thickness of otoliths of sexually dimorphic fishes (Gaemers and Crapon de Crapona 1986). The present study is a contribution to the development of methodology that will be useful in evaluating these and other questions regarding the growth rate and shape of otoliths.

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Appendix 1

Age estimate versus measured fork length and otolith radius by region for red snapper *Etelis carbunculus*.

Northern Marianas			French Polynesia			Hawaiian Islands			Vanuatu		
FL (mm)	Otolith radius (μm)	Est age (yr)	FL (mm)	Otolith radius (μm)	Est. age (yr)	FL (mm)	Otolith radius (μm)	Est. age (yr)	FL (mm)	Otolith radius (μm)	Est. age (yr)
229	4994	3.52	160	5799	4.26	226	6921	5.36	270	4748	3.27
241	3788	2.10	190	6420	4.96	235	7416	5.92	270	4699	3.21
241	2952	1.20	230	6928	5.54	245	7436	5.94	290	4969	3.55
268	4207	2.58	230	6806	5.40	284	7741	6.29	350	5141	3.76
268	4256	2.64	240	7141	5.79	292	8160	6.76	440	5609	4.34
273	4453	2.87	240	8922	7.82	315	8206	6.82	470	6716	5.73
273	4649	3.11	240	7744	6.47	323	8291	6.91	490	6347	5.27
275	4305	2.70	250	6944	5.56	340	8879	7.58	530	6519	5.49
275	3567	1.85	270	8617	7.47	341	8601	7.26	640	8167	7.56
275	4231	2.61	280	8391	7.21	374	8544	7.20	660	7774	7.06
275	4256	2.64	280	7882	6.63	387	8775	7.46	700	9020	8.63
278	4305	2.70	280	8222	7.02	388	9852	8.68	740	8610	8.12
278	4477	2.90	280	8543	7.39	398	10301	9.19	920	9053	8.67
280	4576	3.02	290	8256	7.06	402	10143	9.01			
283	4280	2.67	290	8158	6.95	405	10668	9.60			
283	4330	2.73	290	8496	7.33	407	9985	8.83			
283	3862	2.18	290	8196	6.99	432	10143	9.01			
284	4625	3.08	290	8353	7.17	434	10063	8.92			
284	4305	2.70	290	8726	7.59	437	11193	10.20			
287	4330	2.73	300	8993	7.90	440	10621	9.55			
288	4576	3.02	310	8369	7.18	445	10261	9.14			
289	4551	2.99	320	6847	5.45	458	11350	10.37			
297	4256	2.64	320	8701	7.56	468	10275	9.16			
298	4502	2.93	320	9060	7.97	470	12158	11.29			
298	4428	2.84	330	8538	7.38	475	11043	10.03			
299	4600	3.05	340	9210	8.15	476	11201	10.21			
300	4526	2.96	340	9596	8.58	483	10866	9.83			
302	4428	2.84	340	10084	9.14	484	11347	10.37			
304	4797	3.29	340	8884	7.77	490	10235	9.11			
314	4699	3.17	350	9840	8.86	493	12058	11.18			
314	3567	1.85	350	9624	8.61	515	12094	11.22			
321	4576	3.02	350	9014	7.92	515	11140	10.14			
321	4748	3.23	360	9296	8.24	528	11186	10.19			
329	4797	3.29	360	9719	8.72	582	13527	12.84			
338	5018	3.55	360	8934	7.83	587	12625	11.82			
343	4870	3.37	390	9660	8.66	628	14531	13.98			
354	5166	3.73	400	10010	9.06	641	13457	12.76			
355	5289	3.88	400	10320	9.41						
364	6790	5.69	400	10553	9.67						
367	5092	3.64	400	10576	9.70						
373	4797	3.29	400	10192	9.26						
373	4748	3.23	400	10861	10.03						
374	5338	3.94	410	10110	9.06						
374	5068	3.61	410	11002	10.19						
375	4994	3.52	410	11349	10.58						
375	4969	3.49	410	10996	10.18						
376	4674	3.14	410	10979	10.16						
378	5166	3.73	420	10372	9.47						
400	5609	4.26	430	10473	9.58						
400	5806	4.50	430	10713	9.86						
403	5314	3.91	400	11169	10.38						
404	5756	4.44	450	10384	9.49						
406	4330	2.73	450	12134	11.48						
421	4994	3.52	450	12174	11.52						
426	5289	3.88	460	10551	9.67						
451	5584	4.23	470	9157	8.09						
451	5732	4.41	490	12365	11.74						
451	4526	2.96	500	10034	9.08						
451	4477	2.90	500	10914	10.09						
455	5633	4.29	510	10868	10.03						
455	5658	4.32									
527	6199	4.97									

Abstract.–Seasonal distributions and relative abundances of the Atlantic rock crab *Cancer irroratus*, Jonah crab *C. borealis*, northern lady crab *Ovalipes ocellatus*, and coarsehand lady crab *O. stephensoni* were determined from fish trawl and clam dredge surveys on the continental shelf from Nova Scotia to Cape Hatteras, North Carolina during 1978–87. Rock crabs have the broadest distribution, which includes coastal waters of the Gulf of Maine and depths of 6–456 m from Georges Bank to Cape Hatteras. Jonah crabs are more widely distributed in the Gulf of Maine and on Georges Bank than rock crabs. They occur most frequently in the northern and offshore zones of the middle Atlantic from south of Georges Bank to off Delaware, at depths to over 400 m. Northern lady crabs occur primarily in the inner strata of the middle-Atlantic shelf in depths <27 m, and on shallower portions of Georges Bank. Coarsehand lady crabs occur from southern New Jersey to Cape Hatteras, to over 200 m. *Cancer* spp. occur mainly at 3–18°C, while *Ovalipes* spp. occur mainly at 11–24°C. Sex ratios in rock and Jonah crab catches deviated from 1:1 by season and gear; males dominate in spring trawl surveys, females in summer dredge and fall trawl surveys. Trawl catches of all species were significantly larger at night or twilight than during the day, suggesting more nocturnal activity. Temperature, depth, and their interaction significantly affected the catches of these crabs.

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Distribution and Abundance of Four Brachyuran Crabs on the Northwest Atlantic Shelf

Linda L. Stehlik
Clyde L. MacKenzie Jr.
Wallace W. Morse

Sandy Hook Laboratory, Northeast Fisheries Science Center
National Marine Fisheries Service, NOAA, Highlands, New Jersey 07732

The most common species of brachyuran crabs on the northwest Atlantic continental shelf are the Atlantic rock crab *Cancer irroratus* (subsequently referred to as rock crab), Jonah crab *C. borealis*, northern lady crab *Ovalipes ocellatus*, and coarsehand lady crab *O. stephensoni*. Knowledge of their distributions is incomplete, largely because previous surveys were geographically limited, survey stations were sparse, or surveys were conducted in one season only (Musick and McEachran 1972; Shotton 1973; Haefner 1976, 1977, 1985; Williams and Wigley 1977; Bigford 1979; Williams 1984). No documented information was available on interannual fluctuations in abundance for any of the crabs.

This study was undertaken to investigate shelf-wide seasonal distributions and abundance fluctuations of the four crab species over a ten-year period. Our goals also included providing information about sediments on which the crabs occur, depth ranges, water temperature preferences, size frequencies, sex ratios, and diel catches.

Methods

Data were obtained from groundfish trawl and clam dredge surveys conducted by the Northeast Fisheries Center (NEFSC), National Marine Fisheries Service, over the continental shelf from the northern Gulf of Maine to Cape Hatteras, for the ten-year period 1978 through 1987. The data set consisted of 11,211 stations: 8776 trawls and 2435 dredges. Station locations were selected using a stratified-random design based primarily on depth (Grosslein and Azarovitz 1982, Murawski and Serchuk 1989). Density of trawl stations was 1/500 km^2 for inshore strata (depth <27 m) and 1/1000 km^2 for offshore strata (depth ≥27 m). Clam dredge stations were spaced at 1/460 km^2.

The area covered by trawl surveys in late February–May, designated as spring, and September–November, designated as fall, included the shelf and its upper slope between Nova Scotia and Cape Hatteras. Tow depths in spring and fall were 6–456 m. Trawl surveys in January–February, designated as winter, and July–August, designated as summer, were limited to depths of 6–203 m. Spring and fall trawl surveys were conducted in each of the ten years, winter trawl surveys in 1978 and 1981, and summer trawl surveys from 1978 through 1981. Clam dredge surveys were conducted during winter in December, January, and February (1978–80) and summer in July and August (1978–86) from Georges Bank to Cape Hatteras at depths of 9–110 m (Table 1). Bottom water temperatures were taken at all stations.

In our analysis, the shelf was divided into Gulf of Maine, Georges Bank, and middle-Atlantic subareas (Fig. 1).

Table 1

Groundfish trawl and clam dredge surveys by the NMFS Northeast Fisheries Science Center from Nova Scotia to Cape Hatteras, used in this study. Number of stations (offshore/inshore) used for analysis, and total number of crabs collected, by species, corrected for net or dredge size.

	Trawl				Dredge	
Year	Winter	Spring	Summer	Fall	Winter	Summer
1978	0/[a]78	[a]317/[a]72	168/105	435/77	[b]233/[b]71 [b]75/[b]47	
1979		[a]348/[a]89	145/102	429/89	97/36	
1980		[a]305/[a]100	162/103	270/89	142/62	148/47
1981	86/0	[a]240/[a]90	104/60	255/89		
1982		247/91		285/91		230/69
1983		275/93		308/92		268/128
1984		260/93		341/92		338/110
1985		254/93		266/102		
1986		256/93		262/88		256/78
1987		261/77		236/86		
Total	86/78	2790/891	579/370	3087/895	547/216	1240/432
Rock	340	22916	626	3038	2129	2343
Jonah	8	876	223	883	68	242
Northern lady	0	110	571	3653	1087	936
Coarsehand lady	0	10	47	204	66	185

[a]#41 trawl used; other cruises used #36 trawl.
[b]1.22 m dredge used; other cruises used 1.52 m dredge.

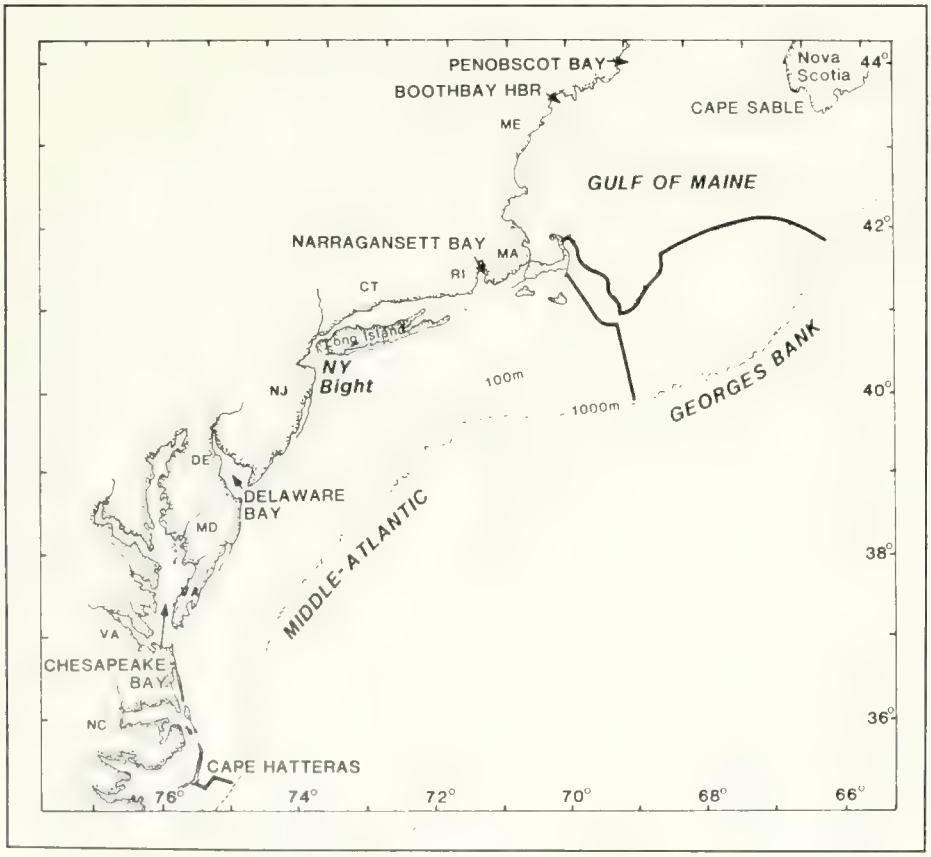

Figure 1

Northwest Atlantic coast and continental shelf with subarea locations mentioned in text.

Locations of stations occupied in the study are plotted by season and gear, cumulatively for all years, in Figures 2a–e. Fall trawl stations were similar in location and number to spring and were not plotted.

The trawlnets used were the #36 and #41 commercial-type otter trawls. The #41 Yankee trawl was used only in spring 1978–81. The #36 Yankee trawl has an opening width of 10.4 m, while the #41 Yankee has an opening width of 11.8 m. In both nets, the mesh size is 12.7 cm stretched with a codend liner of 1.25 cm stretched mesh. Rollers at the front edge of the nets reduce snagging on the bottom. The nets are towed at 6.3 km/hour for 30 minutes per station on a 24-hour basis. Additional details on gear, methods, and sampling area for trawl surveys are described by Grosslein (1969), Grosslein and Azarovitz (1982), Sissenwine et al. (1983), and Survey Working Group, NEFSC (1988).

Crab catches in clam dredge surveys in 1978–86 were used to supplement the trawl data. Dredges used in 1978 were 1.22 m wide; since 1979, they have been 1.52 m wide. Both have 5 cm mesh bags (Murawski and Serchuk 1989). The dredges employ jets of water at their openings to loosen sediments, and are towed at 2.7 km/hour for 4 minutes (1.22 m dredge) or 5 minutes (1.52 m dredge) per station, on a 24-hour basis.

Catchability factors were used to standardize the catches for the two trawlnets and the

Figure 2

Cumulative station locations: (a) winter trawl, (b) winter dredge, (c) spring trawl (fall trawl similar but not shown), (d) summer dredge, (e) summer trawl.

two clam dredges used. The #41 trawl catches were divided by 1.79, the ratio of catch-per-tow of *Cancer* spp. by the #41 net to the #36 net on the RV *Albatross IV* (Sissenwine and Bowman 1978), to equate them to the #36 trawl catches. The 1.22 m dredge catches were multiplied by 1.56 [(1.52/1.22)(5/4)] (S.A. Murawski, NMFS Woods Hole Lab., Northeast Fish. Sci. Cent., Woods Hole, MA, pers. commun., Oct. 1987) to make them comparable with catches of the 1.52 m dredge.

Carapace widths, measured between the tips of the anterolateral spines, were determined at sea for all specimens. When occasional collections totaled more than 100 crabs of one species, a random subsample of about 100 was measured and sexed, and the results expanded to estimate total catch. Width frequencies are presented from trawl collections only, because dredge collections included few crabs <5 cm.

Data on sex were available for rock crabs and Jonah crabs from all surveys. Sexes of northern lady crabs and coarsehand lady crabs were available from winter dredge surveys only.

For analysis of the relative abundance of crabs, the survey area was divided into five strata, i.e., Gulf of Maine offshore and inshore, Georges Bank, and middle-Atlantic offshore and inshore. The mean and variance of catch-per-tow in each stratum were estimated using the delta distribution, which considers the lognormally transformed catch at positive tows, i.e., tows with crabs (Pennington 1983). Estimates for the five strata were combined by weighting by stratum area in km^2 using equations for stratified mean and variance (Survey Working Group, NEFSC 1988). Trawl and dredge data were handled separately. Weighted estimates of abundance were obtained by sex, time of capture, and bottom temperature for each species of crab. Relative abundances in numbers and weight were calculated by year from fall surveys, because the same size net was used each year.

To examine diel variability in catch, the stations were divided into four groups, i.e., dawn, day, dusk, and night, using the starting time of tow. For each season, two 4-hour periods of low light were defined, and the remaining hours were full light and full dark. For example, for dawn in winter the earliest and latest times of sunrise were determined for all months and latitudes of the survey, and 1 hour was added before and after, to yield a 4-hour period. For winter surveys, periods were, in hours: dawn 0501–0900, day 0901–1500, dusk 1501–1900, night 1901–0500. For spring and fall surveys, hours: dawn 0401–0800, day 0801–1600, dusk 1601–2000, and night 2001–0400. For summer surveys, hours: dawn 0301–0700, day 0701–1700, dusk 1701–2100, and night 2101–0300. Weighted estimates of abundance by time period were compared by analysis of variance for unequal sample size (the GT2 multiple comparison method in Sokal and Rohlf 1981).

For rock and Jonah crabs, sex ratio was calculated by dividing the weighted mean abundance of males by that of females. The mean abundances of each sex were compared by t tests.

We used stepwise regression analysis to fit linear models of abundance (all species) and sex ratio (rock and Jonah crabs) by the independent variables of depth, temperature, and their interaction, using the method of least squares (SAS Institute Inc. 1985). The dependent variables were transformed to logarithms as ln [abundance + 1] and ln [abundance of males/abundance of females]. The data were fit by seasons and subareas.

Results and discussion

Distribution and abundance

Rock crabs Rock crabs were distributed throughout the shelf, with their center of abundance extending from Georges Bank to Cape Hatteras in depths of 6–456 m (Figs. 3a–b, 4a–d). The principal sediments in that area are sand and sand/gravel (Uchupi 1963, Schlee 1973). Previous studies found rock crabs also on rocky (Scarratt and Lowe 1972) and muddy (Krouse 1980) sediments, and on blue mussel *Mytilus edulis*, (Reilly and Saila 1978), oyster *Crassostrea virginica*, and shell beds (C.L. MacKenzie Jr., unpubl. data).

Seasonal distribution patterns of rock crabs in the middle-Atlantic subarea show that they migrate across much of the shelf, moving inshore during cold months and offshore during warm months. Winter surveys show rock crabs concentrated in depths <40 m, with only scattered occurrences farther offshore (Fig. 3a–b). In spring, their distribution remained essentially unchanged (Figs. 4a, 5). In spring trawl surveys, inshore stations averaged 22.3 crabs per tow whereas offshore stations averaged only 1.1 crabs per tow (Table 2). Later in the year, part of the population moves offshore, resulting in a more even distribution on the shelf during summer and fall (Figs. 4b–d, 5). Catch-per-tow during the fall trawl surveys averaged 1.2 crabs at inshore stations and 0.9 crabs at offshore stations (Table 2).

In the Gulf of Maine, rock crabs occurred only in coastal zones from spring through fall (Fig. 4a–d; Table 2). We have no data on the winter distribution of rock crabs in that subarea, but Krouse (1972, 1976, 1980) reported that they occupy coastal zones year-round in Maine.

Triggering cues for seasonal migrations in the middle-Atlantic are unknown, but they are apparently related to seasonal cooling and warming. Terretta

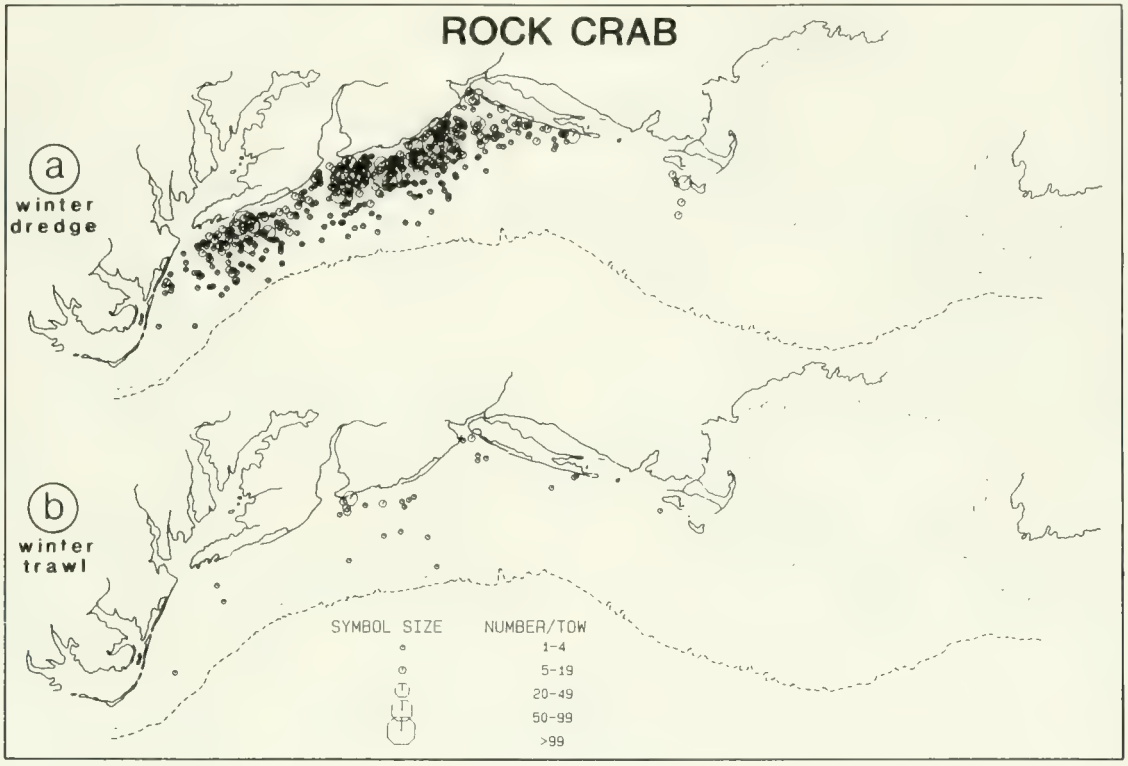

Figure 3
Rock crab distribution from winter dredge and winter trawl surveys.

(1973) reported that rock crabs enter Chesapeake Bay in the fall, when temperatures are below 12°C, and exit in the spring before they rise to 12°C. Although rock crabs have been caught at temperatures as high as 25°C (Williams and Wigley 1977), our data show that they tend to avoid temperatures above 18°C (Fig. 6). They were most abundant in spring in temperatures of 4–7°C, and in fall at 8–18°C. In previous trawl surveys, most rock crabs were caught at 0–14°C (Musick and McEachran 1972, Haefner 1976), but less sampling was done at higher temperatures.

Mean catch-per-tow by number and weight in fall varied among years (Fig. 7). The year of peak catches, 1986, produced nearly 20 times more rock crabs than in the lowest catch year, 1978. However, the decadal data set revealed no consistent trend in abundance. The highest catches by weight were in 1981 and 1986; the year 1986 was unusual in that 60% of the crabs were ≤5 cm carapace width. The mean weight per crab was 35 g in 1986, but averaged 63 g in all other years combined.

Size frequencies of rock crabs differed by subarea and sex (Fig. 8). Modal carapace widths of males and females in the Gulf of Maine and middle-Atlantic peaked at 7–9 cm. The largest crabs in both subareas were males. On Georges Bank, they were smaller; widths of both sexes peaked at 4 cm.

Weighted mean catch-per-tow of rock crabs by trawls was highest at night in spring and at twilight in summer and fall (Table 3). We assume that crabs on the bottom can be caught by trawls, but crabs buried in sediments can be captured only by clam dredges. Nocturnal activity in rock crabs was reported by MacKenzie (1981), who observed that rock crabs are buried at times during the day, but not at night. Fogarty (1976) and Rebach (1987) found that rock crabs exposed to artificial photoperiods are more active in dark than in light periods. Dredge catches of rock crabs also fluctuated by time of day, but the effect of light upon catchability of crabs by dredges is unknown.

Abundances of males and females were significantly different for all gears and seasons (Table 4). Males outnumbered females in spring and summer trawl surveys, whereas females outnumbered males in fall trawl and all dredge surveys. In contrast, Shotton (1973) and Haefner (1976) found that males usually outnumbered females in late-spring and fall surveys off Virginia.

Figure 4
Rock crab distribution from spring trawl, summer dredge, summer trawl, and fall trawl surveys.

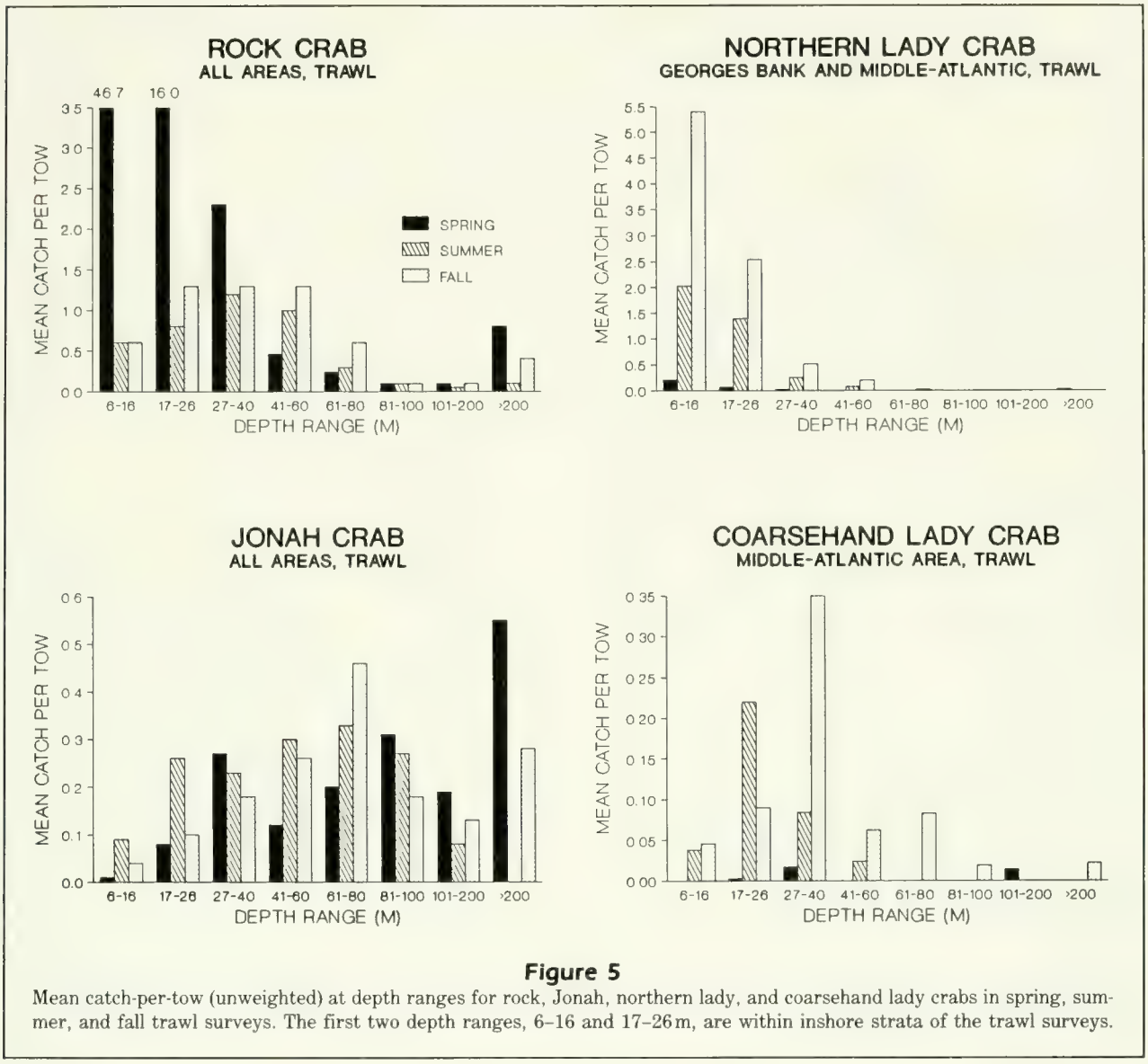

Figure 5

Mean catch-per-tow (unweighted) at depth ranges for rock, Jonah, northern lady, and coarsehand lady crabs in spring, summer, and fall trawl surveys. The first two depth ranges, 6–16 and 17–26 m, are within inshore strata of the trawl surveys.

In the middle-Atlantic, male rock crabs were distributed closer to shore than females. A larger proportion of males occurred inshore than offshore in spring and summer trawl surveys, and a larger proportion of females occurred offshore than inshore in dredge surveys (Fig. 9). Males are also dominant in estuaries such as lower Delaware Bay (Winget et al. 1974) and lower Chesapeake Bay (Terretta 1973), where they overwinter (Haefner and Van Engel 1975), and along the Virginia coast (Shotton 1973).

While different migratory patterns of the sexes might partially account for the unequal sex ratios in rock crab catches in this study, we consider differences by sex in availability to sampling gear to be largely responsible. Comparing catches of rock crabs in winter dredge surveys with spring trawl surveys, both of which were conducted during the cold season, significantly more females were caught than males by dredges, whereas significantly more males than females were caught by trawls (Table 4). This suggests that females bury more than males. The two summer surveys showed the same phenomenon. Our spring trawl data showed the ratio of males to females was lowest at night (Fig. 10), from which we conclude that diel activity rhythms at that season may be different by sex, and that females are more active at night than by day. They would be buried when inactive during daylight hours.

Inactivity of females may be related to the reproductive cycle. Females extrude eggs in fall, which are

Table 2

Catch-per-tow (delta mean and standard error) of each crab species, 1978–87, by gear, quarter, and strata (Off = offshore, In = inshore), and weighted delta mean and standard error for all strata. Corrected for #41 trawlnet and 1.22 m clam dredge. All stations except winter trawl included.

		Trawl						Dredge			
		Spring		Summer		Fall		Winter		Summer	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Rock crab											
Gulf of Maine	Off	0.03	(0.010)	0.05	(0.030)	0.02	(0.006)	no stations		no stations	
	In	2.24	(0.849)	1.24	(0.403)	0.84	(0.179)	no stations		no stations	
Georges Bank	Off	0.07	(0.013)	0.67	(0.216)	0.56	(0.689)	no stations		0.59	(0.096)
Middle Atlantic	Off	1.12	(0.130)	0.83	(0.091)	0.93	(0.071)	2.25	(0.195)	1.61	(0.079)
	In	22.34	(2.215)	0.58	(0.072)	1.15	(0.133)	5.27	(0.536)	0.76	(0.071)
All strata		2.64	(0.004)	0.61	(0.002)	0.56	(0.001)	2.88	(0.007)	1.22	(0.001)
Jonah crab											
Gulf of Maine	Off	0.10	(0.014)	0.10	(0.042)	0.06	(0.010)	no stations		no stations	
	In	0.33	(0.154)	0.26	(0.121)	0.29	(0.078)	no stations		no stations	
Georges Bank	Off	0.13	(0.020)	0.14	(0.040)	0.13	(0.014)	no stations		0.22	(0.049)
Middle Atlantic	Off	0.44	(0.041)	0.34	(0.059)	0.48	(0.041)	0.09	(0.019)	0.14	(0.021)
	In	0.08	(0.024)	0.21	(0.064)	0.09	(0.017)	0.08	(0.048)	0.08	(0.026)
All strata		0.23	(0.0003)	0.23	(0.001)	0.23	(0.0002)	0.09	(0.001)	0.15	(0.0004)
Northern lady crab											
Georges Bank	Off	no crabs		0.07	(0.029)	0.10	(0.021)	no stations		0.28	(0.065)
Middle Atlantic	Off	<0.01	(0.003)	0.17	(0.052)	0.11	(0.023)	0.17	(0.039)	0.12	(0.018)
	In	0.11	(0.018)	1.53	(0.180)	3.36	(0.351)	3.01	(0.688)	1.43	(0.163)
All strata		0.03	(0.0001)	0.38	(0.002)	0.62	(0.001)	0.76	(0.005)	0.36	(0.001)
Coarsehand lady crab											
Middle Atlantic	Off	0.01	(0.004)	0.07	(0.035)	0.13	(0.026)	0.10	(0.023)	0.15	(0.025)
	In	<0.01	(0.001)	0.08	(0.034)	0.06	(0.014)	0.05	(0.025)	0.08	(0.028)
All strata		0.01	(0.0001)	0.07	(0.001)	0.11	(0.001)	0.09	(0.001)	0.10	(0.0004)

carried until hatching in spring (Krouse 1972). Conversely, perhaps some of the more active males avoid a slowly towed dredge but cannot avoid a trawl because it is too large. Haefner's (1976) trawl surveys, which showed significantly more males than females, must have caught the active males and missed the buried females.

There are a few possibilities as to why rock crabs in the middle-Atlantic migrate inshore in fall and remain until spring. Perhaps they do so to feed when potential competitors for prey, such as the blue crab *Callinectes sapidus* and northern lady crab, both of which occur inshore, are dormant in winter. Rock crabs are the only brachyurans in the subarea which molt in winter (Haefner and Van Engel 1975), and it is possible that they migrate inshore to avoid fishes which could prey on them while they are in the vulnerable soft and paper-shell stages. The latter stage in adults persists for two to three months (Haefner and Van Engel 1975). Another possibility is that their larval stages survive better in coastal zones when released in spring.

The environmental variables that accounted for the largest proportion of the variance of rock crab abundance in the middle-Atlantic subarea were depth in spring and temperature in summer and fall (Table 5). The slope of the regression of depth upon abundance was negative in that subarea in all seasons and was strongest in spring (compare with Figure 5). Temperature was also negatively correlated with rock crab abundance in that subarea. In the Gulf of Maine, depth and the cross-product, depth * temperature, had the

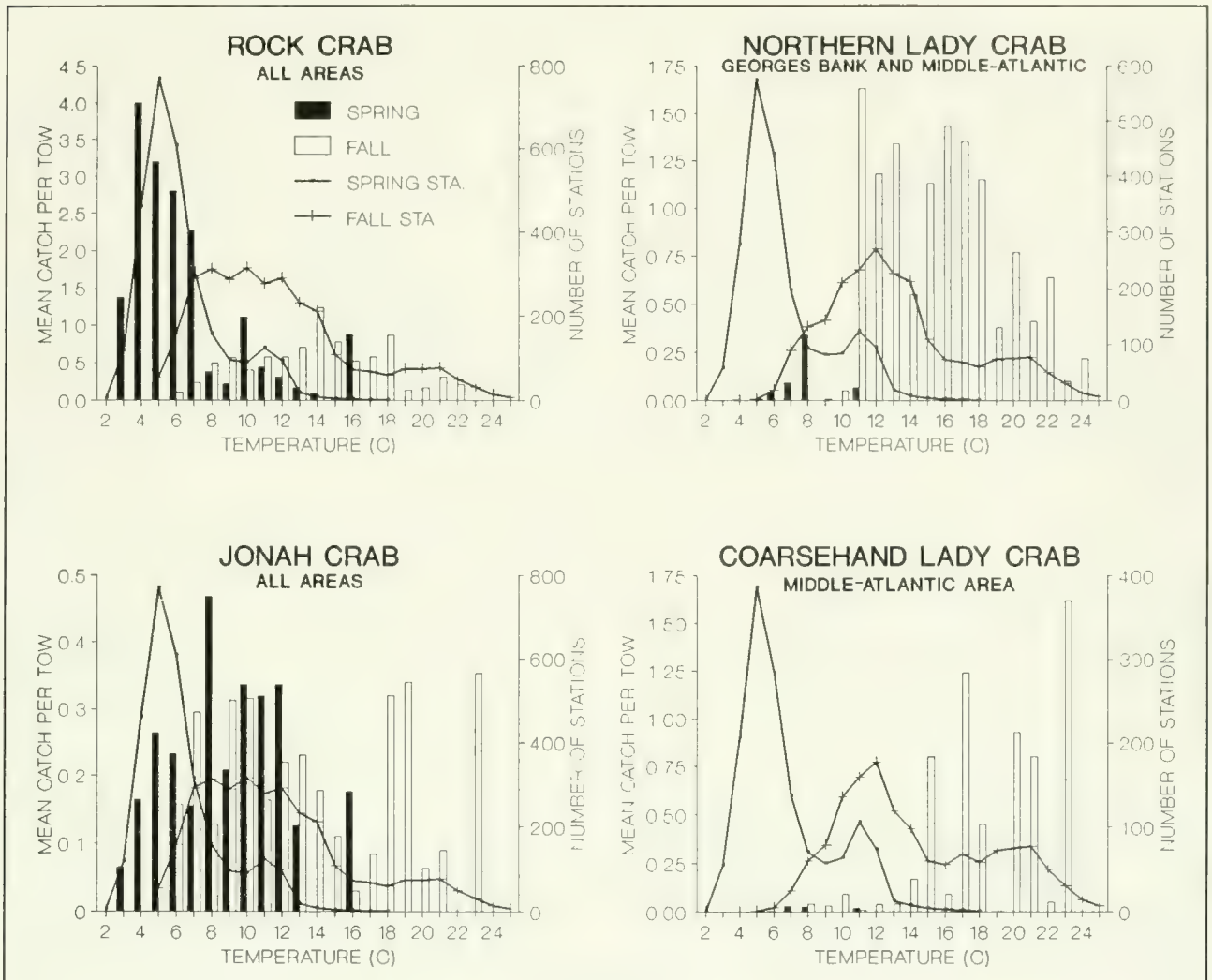

Figure 6

Mean abundance (unweighted) at bottom-water temperatures from spring and fall trawl surveys, with number of stations (lines) at each temperature.

highest partial correlation with abundance. On Georges Bank, the most important variable was temperature in summer and fall. In both subareas, temperature was positively correlated with rock crab abundance. Sex ratio was significantly associated with depth * temperature (R, −0.355) and depth (R, +0.245) in fall; however, no variables were significant in spring or summer.

Jonah crabs Jonah crabs were distributed on the shelf and its upper slope from Penobscot Bay, Maine, and Cape Sable, Nova Scotia, southward to Cape Hatteras, but were sparse south of Delaware (Fig. 11a–d). Jonah crabs were less abundant than rock crabs on Georges Bank and in the middle-Atlantic. They occurred in all surveyed depths, but were least abundant in 6–16 m (Fig. 5). The sediment where most Jonah crabs occur is silty sand (Uchupi 1963, Schlee 1973). They have also been collected on gravel and rocky sediments (Jeffries 1966, Krouse 1980).

A comparison of distributions in Figure 11 suggests that Jonah crabs migrate toward the offshore edges of the shelf in Georges Bank and the middle-Atlantic subarea in winter and into their central portions in summer. Observations in the coastal zone of Maine (Krouse 1980) and in Narragansett Bay (Jeffries 1966), where Jonah crabs were present in summer but not in winter, confirm that seasonal migrations probably occur. However, data on offshore and inshore catch-per-tow (Table 2) and depth range (Fig. 5) show that migrations may

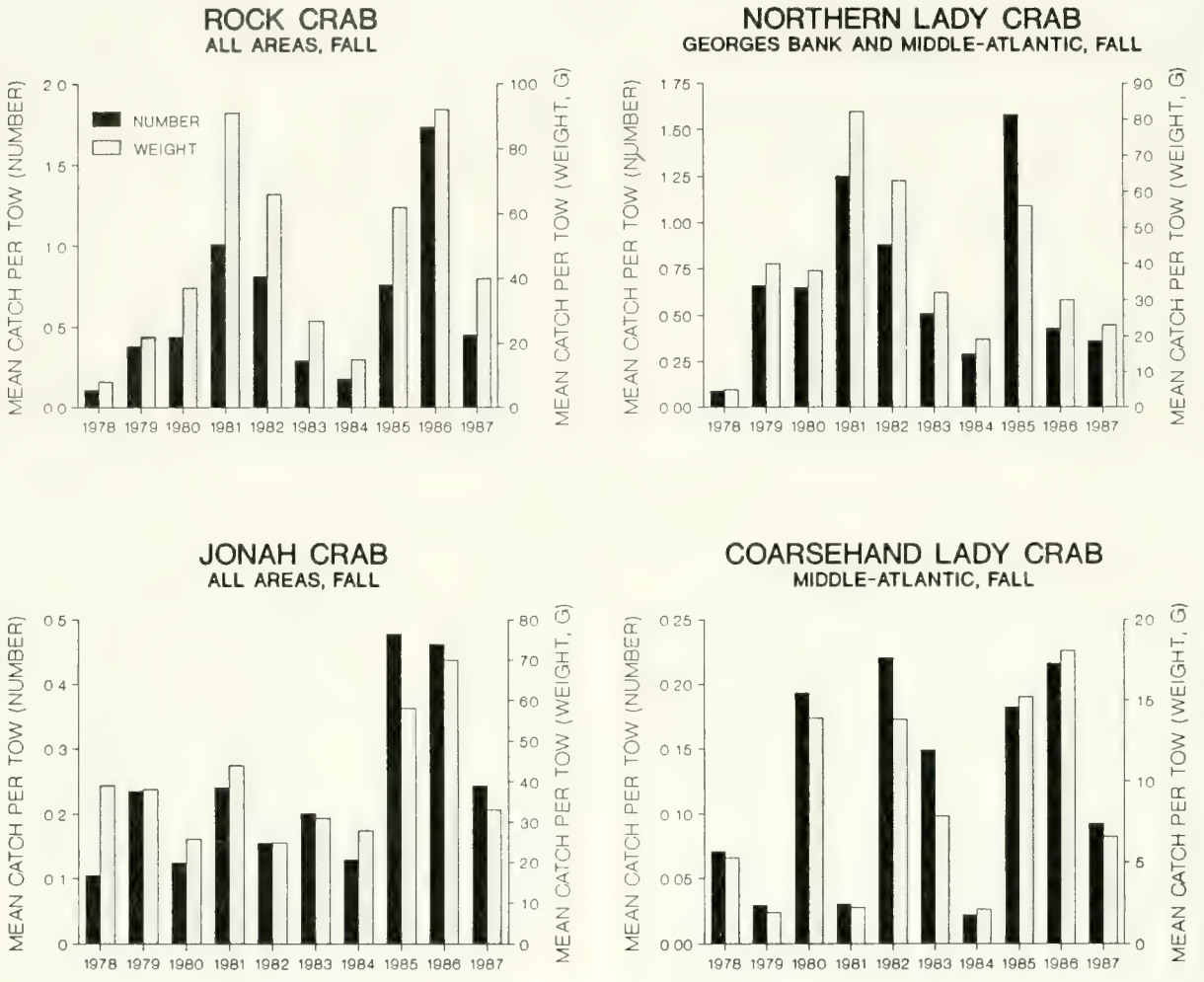

Figure 7
Weighted mean catch-per-tow by number and weight (g), by year. Data are from fall trawl surveys.

be minor, and much less extensive than in the rock crab.

Jonah crabs were collected at temperatures of 3–23°C (Fig. 6). Similarly, Haefner (1977) collected Jonah crabs in the middle-Atlantic over a temperature range of 6–24°C at depths of 150–400 m, while maximum abundance of the species was from 8–14°C. Krouse (1980) concluded that Jonah crabs have a narrower temperature tolerance than rock crabs. We found no difference in the annual temperature ranges of the two species. However, in spring, the majority of rock crabs occurred at 3–7°C when they were concentrated inshore, while the majority of Jonah crabs occurred at 8–12°C because they were mostly offshore.

The scarcity of Jonah crabs off the coasts of Maryland, Virginia, and North Carolina (Fig. 11) may be due to unfavorably high temperatures. Average bottom temperatures in that area in August and September are 18–23°C. At those latitudes, Jonah crabs were more abundant on the outer shelf and slope, where temperatures are mostly 14–18°C during those months (Mountain and Holzwarth 1989).

Mean catch-per-tow by number and weight varied among years (Fig. 7). It was roughly similar during 1978–84 and in 1987. However, it was nearly twice as high in the years 1985 and 1986.

Carapace widths of Jonah crabs differed by sex. In all three subareas, males had a broad range of widths, while females had sharp modal peaks of 10, 12, and 8 cm, in the Gulf of Maine, Georges Bank, and middle-Atlantic, respectively (Fig. 8). Few females attained widths of >13 cm. These size ranges correspond to

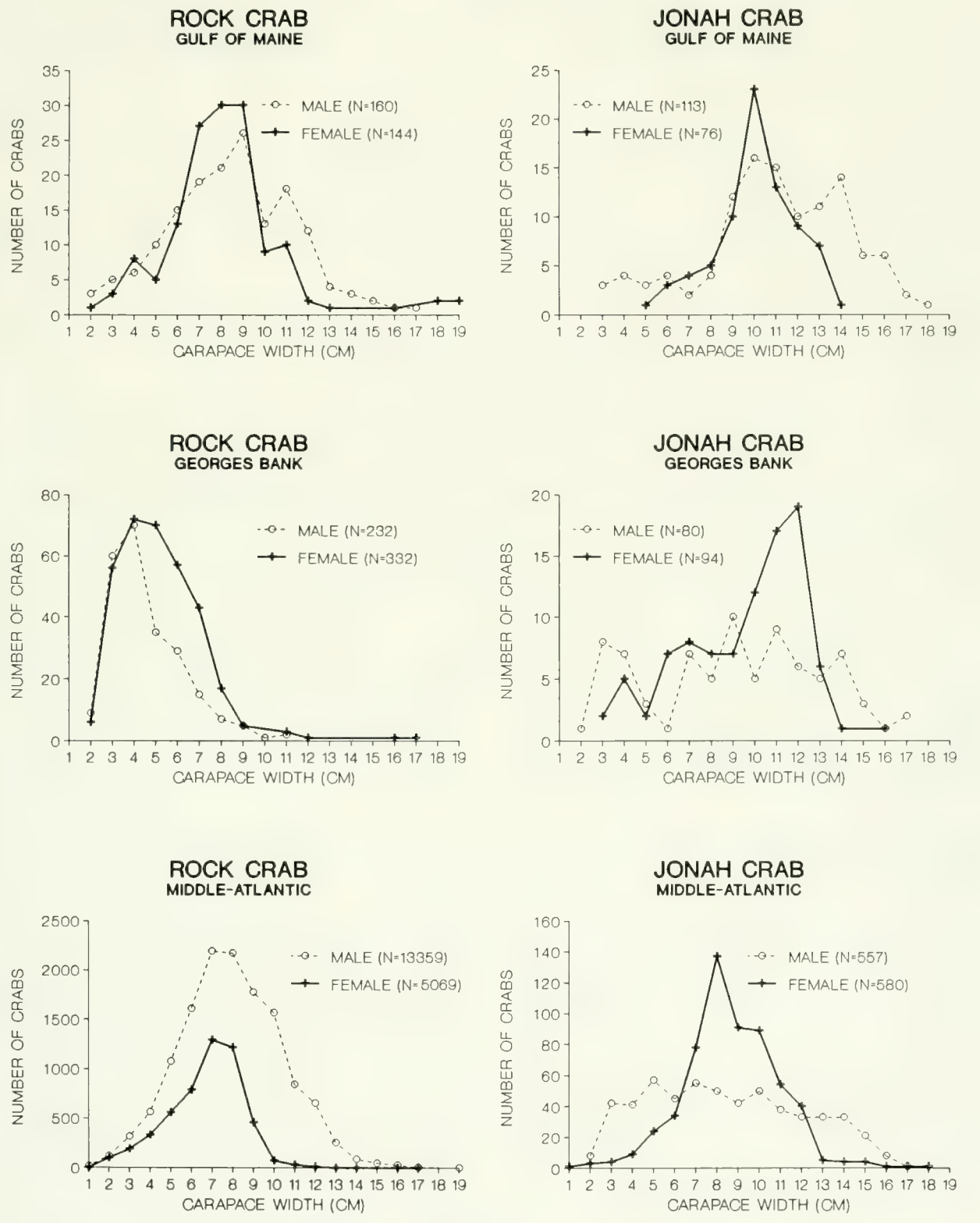

Figure 8

Carapace width-frequency distributions of combined spring and fall trawl-caught rock, Jonah, northern lady, and coarsehand lady crabs.

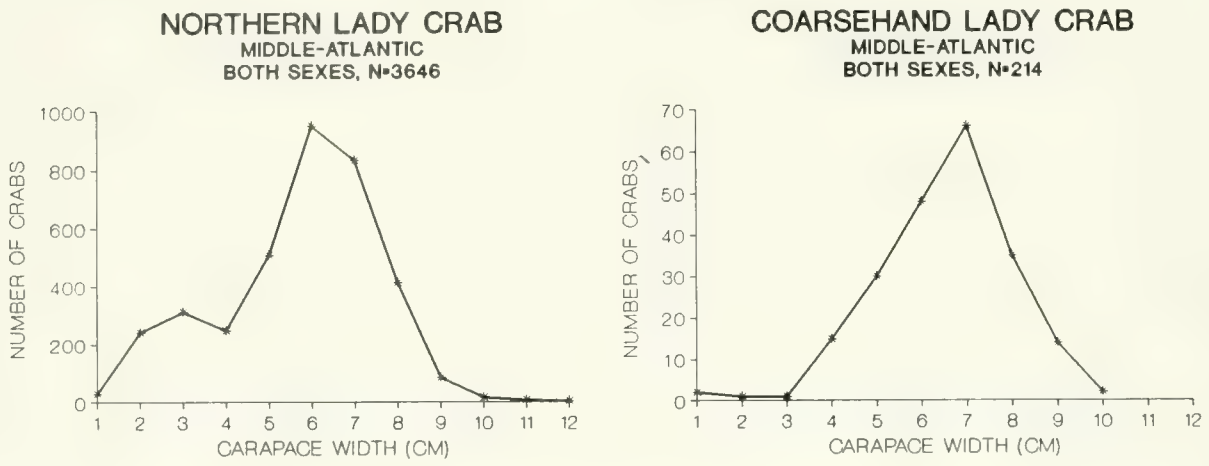

Figure 8 (continued)

Table 3

Catch-per-tow (weighted delta means and standard errors) of crabs by time of day, with number of crabs included. Time periods as defined in Methods. Day, night, and twilight catch-per-tow were significantly different by GT2 multiple comparison tests ($P<0.05$) within species, gear, and season, in all cases except two: in rock and Jonah crabs in winter, two groups were not statistically different and are noted with superscripts a and b. Number of stations as in Table 2.

	Trawl						Dredge			
	Spring		Summer		Fall		Winter		Summer	
Species/period	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Rock crab										
Day	2.25	(0.0112)	0.612	(0.0047)	0.375	(0.0011)	4.84	(0.072)	1.26	(0.0032)
Night	3.20	(0.0102)	0.460	(0.0053)	0.636	(0.0015)	[a]3.78	(0.032)	1.04	(0.0045)
Twilight	2.31	(0.0103)	0.727	(0.0067)	0.647	(0.0018)	[a]3.74	(0.045)	1.31	(0.0043)
No. crabs	22916		626		3038		2163		2343	
Jonah crab										
Day	0.206	(0.0008)	0.241	(0.0025)	0.200	(0.0007)	[b]0.129	(0.0064)	0.163	(0.0011)
Night	0.300	(0.0010)	0.291	(0.0056)	0.253	(0.0008)	0.088	(0.0016)	0.178	(0.0020)
Twilight	0.190	(0.0006)	0.183	(0.0021)	0.229	(0.0007)	[b]0.144	(0.0064)	0.112	(0.0009)
No. crabs	876		223		883		53		242	
Northern lady crab (Georges Bank and middle-Atlantic subareas only)										
Day	0.013	(0.0001)	0.376	(0.0054)	0.272	(0.0012)	0.447	(0.0118)	0.344	(0.0016)
Night	0.027	(0.0003)	0.499	(0.0077)	0.797	(0.0044)	0.748	(0.0106)	0.372	(0.0037)
Twilight	0.019	(0.0002)	0.329	(0.0040)	0.891	(0.0044)	0.820	(0.0185)	0.393	(0.0028)
No. crabs	110		571		3653		447		936	
Coarsehand lady crab (Middle-Atlantic subarea only)										
Day	0.004	(0.0001)	0.016	(0.0007)	0.030	(0.0004)	0.051	(0.0034)	0.118	(0.0011)
Night	0.014	(0.0003)	0.057	(0.0025)	0.140	(0.0014)	0.116	(0.0031)	0.188	(0.0031)
Twilight	0.001	(0.0001)	0.151	(0.0062)	0.155	(0.0018)	0.132	(0.0046)	0.107	(0.0015)
No. crabs	10		47		204		49		185	

Figure 9 (facing page)
Sex ratios (abundance males:abundance females) of rock and Jonah crabs, by season and offshore/inshore strata, middle-Atlantic subarea.

Figure 10 (facing page)
Sex ratios (abundance males:abundance females) of rock and Jonah crabs by time of day, all subareas combined.

Table 4

Catch-per-tow (weighted delta means and standard errors) of male and female rock and Jonah crabs, by gear and season, significance (S) ($P<0.01$) by t tests, sex ratio (male:female), and total number of crabs sexed (corrected for net and dredge size). Number of stations sampled as in Table 2.

	Trawl						Dredge			
	Spring		Summer		Fall		Winter		Summer	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Rock crab										
Males	1.211	(0.0019)	0.229	(0.0010)	0.235	(0.0002)	0.711	(0.0020)	0.402	(0.0005)
Females	0.457	(0.0005)	0.196	(0.0009)	0.275	(0.0003)	1.603	(0.0051)	0.782	(0.0010)
Significance	S		S		S		S		S	
Sex ratio	2.6:1		1.2:1		1:1.2		1:2.2		1:1.9	
No. crabs	16666		432		2657		2126		2226	
Jonah crab										
Males	0.119	(0.0002)	0.072	(0.0005)	0.087	(0.0001)	0.041	(0.0004)	0.045	(0.0002)
Females	0.073	(0.0001)	0.074	(0.0005)	0.121	(0.0002)	0.027	(0.0003)	0.103	(0.0003)
Significance	S		NS		S		S		S	
Sex ratio	1.6:1		1:1.0		1:1.4		1.5:1		1:2.3	
No. crabs	718		144		783		54		234	

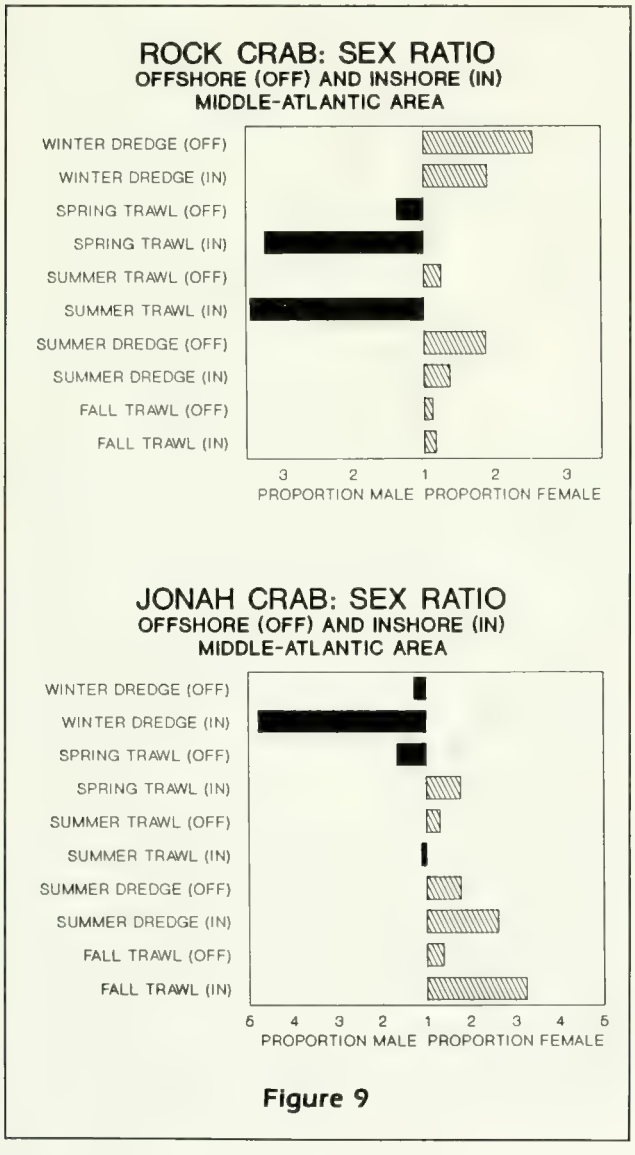

Figure 9

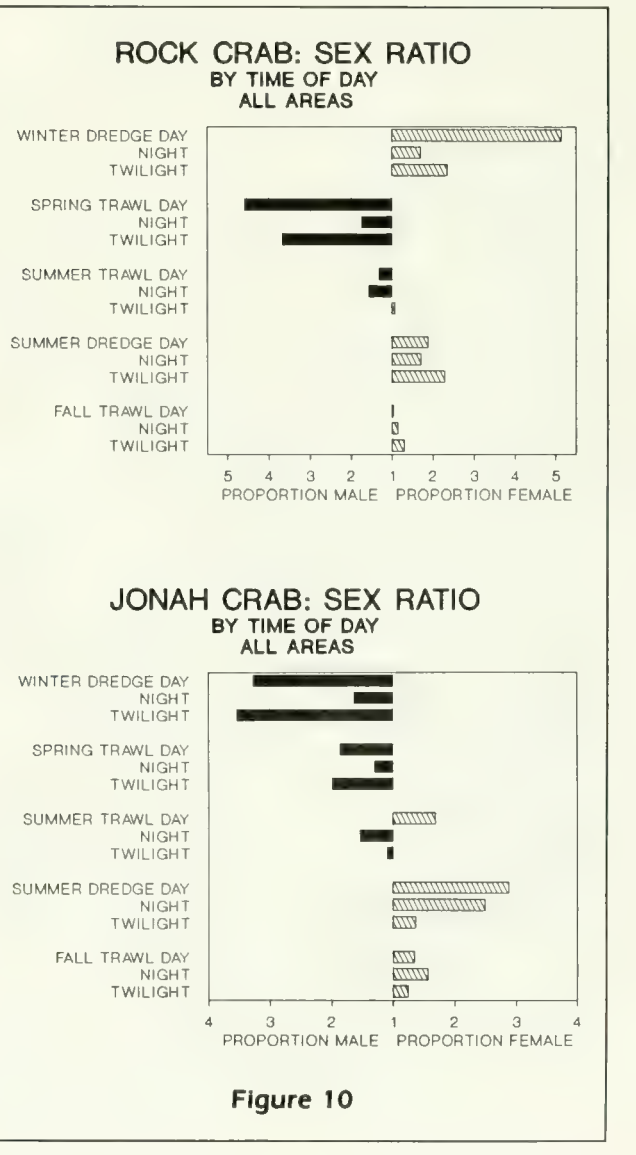

Figure 10

Table 5

Partial correlation coefficients (R) and model R^2 of depth, temperature, and their interaction upon abundance of crabs, determined by regression analysis. Shown when significant to $P<0.05$; dashes = not significant. Slope of R is positive unless sign is negative. Data are from spring, summer, and fall trawl surveys, Gulf of Maine (GM), Georges Bank (GB), and middle-Atlantic (MA); a = no crabs.

	Spring			Summer			Fall		
	GM	GB	MA	GM	GB	MA	GM	GB	MA
No. stations	817	590	2877	161	187	881	893	746	3069
Rock crab									
Depth	−0.230	—	−0.316	—	—	−0.140	0.259	0.098	−0.093
Temperature	0.162	—	−0.225	—	0.319	−0.185	0.119	0.232	−0.129
Depth * Temperature	—	—	0.129	−0.350	—	0.089	−0.240	−0.126	—
Model R^2	0.079	—	0.167	0.122	0.102	0.062	0.139	0.079	0.025
Jonah crab									
Depth	—	—	0.319	−0.198	—	0.186	0.074	—	0.099
Temperature	—	—	—	—	0.158	—	0.120	—	−0.182
Depth * Temperature	—	0.200	−0.131	—	—	—	−0.066	—	—
Model R^2	—	0.040	0.119	0.039	0.025	0.034	0.024	—	0.043
Northern lady crab									
Depth	a	a	−0.093	a	0.202	−0.365	a	0.162	0.072
Temperature			—		0.265	0.165		0.222	0.271
Depth * Temperature			0.067		—	—		−0.078	−0.147
Model R^2			0.013		0.124	0.167		0.082	0.101
Coarsehand lady crab									
Depth	a	a	—	a	a	—	a	a	—
Temperature			—			0.161			0.080
Depth * Temperature			—			—			—
Model R^2			—			0.026			0.006

those reported earlier for the Gulf of Maine (Krouse 1980) and middle-Atlantic (Haefner 1977).

Trawl catches of Jonah crabs were highest at night in spring, summer, and fall, suggesting diel activity cycles similar to those of rock crabs (Table 3). Under artificial photoperiods, Jonah crabs are active only in the dark period, with peak activity at dusk (Fogarty 1976). Our data also show differences in sex ratio by time of day, especially in spring (Fig. 10), suggesting differences in diel activity between the sexes.

Male Jonah crabs were significantly more abundant than females in spring trawl surveys, whereas females were significantly more abundant in fall (Table 4). These results are very similar to the findings of Haefner (1977) for Jonah crabs off Virginia. Males dominated the dredge catch in winter, though sample size was small; females dominated the dredge catch in summer. Seasonal changes in sex ratio may be due to limited single-sex migrations or differences in catchability reflective of the reproductive cycle.

In the Gulf of Maine, from a limited number of individuals in this study, the sex ratio in spring trawl collections was 4.5:1 males and in fall 1.2:1 females. Krouse (1980) found that in coastal Maine, males dominated the catch in lobster pots in July and females in August and September. He concluded that female Jonah crabs occupy shallow zones during the latter two months to molt and copulate.

Differences in sex ratios of Jonah crabs offshore and inshore in the middle-Atlantic were unlike those of rock crabs (Fig. 9). Considering spring and fall, when sample size was largest, the ratio of females to males was higher inshore than offshore. In contrast, in depths greater than 200 m, males outnumbered females in both seasons. In contrast, in Haefner's (1977) fall survey, sex ratios favored males from 41–60 m depths and females from 61 m to the survey limit of 260 m.

Most of the partial correlation coefficients of the environmental variables versus the catches in numbers were lower for Jonah crabs than for rock crabs (Table 5). Perhaps this was because Jonah crabs were distributed rather evenly across all temperatures and depths (Figs. 5, 6). In the middle-Atlantic, their abundance was

Figure 11
Jonah crab distribution, from winter dredge, spring trawl, summer dredge, and fall trawl surveys.

most highly correlated with depth in spring, but positively, unlike that of rock crabs. In that subarea, their abundance was negatively correlated with temperature in fall, with a minor effect of depth. No significant associations were found between the sex ratios and environmental variables.

Figure 12
Northern lady crab distribution, from winter dredge, spring trawl, summer dredge, and fall trawl surveys.

Northern lady crabs Northern lady crabs were distributed on the inner middle-Atlantic shelf and Georges Bank, mostly in depths <27 m (Figs. 5, 12a–d). They were concentrated on the inner shelf from the eastern tip of Long Island southward. Two other pockets of concentration in summer and fall were on the shoals

south of Nantucket Island, and on the shallow portion of Georges Bank. Catch-per-tow was highest on the inshore stratum of the middle-Atlantic, where it was over ten times offshore catch-per-tow (Table 2). Northern lady crabs have been observed in densities as high as 3–4/m^2 within 2km of the New Jersey coast (MacKenzie et al. 1985). The sediments where northern lady crabs are found are fine-to-medium sand or gravelly sand (Uchupi 1963). Williams (1984) found this species on a variety of sediments, mostly sand.

This study supports the speculation by Musick and McEachran (1972) that northern lady crabs may be inactive or buried in winter. As stated above, we hypothesize that dredges catch buried crabs that trawls do not. In our 1978 winter trawl survey in the middle-Atlantic, which included 78 stations, no northern lady crabs were collected, but in the 1978 winter dredge survey in the same area, which included 133 stations, 240 were collected. Moreover, in spring trawl surveys, during which water temperatures had not risen appreciably since winter, this crab was rarely collected.

Northern lady crabs were caught with trawls where temperatures were 4–24°C; 96% were caught where temperatures were 11.0°C and above (Fig. 6). Along the New Jersey coast, Grant (1987) found northern lady crabs were abundant in summer but absent when temperatures dropped below 18°C. This crab was not found in the Gulf of Maine; temperatures there are mostly 4–10°C (Mountain and Holzwarth 1989).

Mean catch-per-tow varied substantially among years. The catch was relatively low in 1978; in contrast, the mean weight of crabs was about 16 times higher in 1981, the peak year (Fig. 7). In 1985, the mean weight per crab was 29g, when an unusually large number of small crabs were present on Georges Bank and in the middle-Atlantic. For all other years combined, the mean weight per crab was 58g.

The modal carapace width of northern lady crabs was 6cm (Fig. 8). From winter dredge surveys, for which sex information was available, modes were 7cm in males and 6cm in females. The ratio of abundance of males to females was 1.1:1 (N 427) at that time.

The abundance of northern lady crabs was significantly different by time of day, i.e., highest at night or twilight in trawl surveys (Table 3). Similarly, in a laboratory study this species was most active at dusk and night (Sponaugle and Lawton 1990).

The abundance of northern lady crabs was negatively correlated with depth in spring and summer in the middle-Atlantic (Table 5). In summer and fall, it was positively correlated with temperature. In fall, depth had a weak, positive partial correlation with catches, although if considered alone, depth correlated negatively. On Georges Bank, the abundance of northern lady crabs was positively correlated with temperature and depth in summer and fall.

Coarsehand lady crabs Coarsehand lady crabs were distributed across the middle-Atlantic from southern New Jersey to Cape Hatteras in depths to 293m (Fig. 13a–d). The range of this species was reported previously as from Accomac County, Virginia, to Biscayne Bay, Florida (Wenner and Read 1982, Williams 1984, Haefner 1985). The principal sediment from New Jersey to Cape Hatteras is sand (Uchupi 1963). Williams (1984) also reported that this crab occurs on sand.

The distributions of coarsehand and northern lady crabs overlapped, but coarsehand lady crabs were distributed farther offshore (Fig. 5), as Musick and McEachran (1972) and Williams (1984) reported. Abundance of coarsehand lady crabs peaked at depths of 27–40m. Coarsehand lady crabs were less abundant than northern lady crabs in the middle-Atlantic inshore stratum (Table 2), as Dudley and Judy (1971) observed off the North Carolina coast. Both species were about equally abundant in the offshore stratum.

Coarsehand lady crabs were collected at temperatures of 6–23°C, but only about 5% occurred at temperatures below 14°C (Fig. 6). The temperature range of this species is narrower than that of the northern lady crab.

As in the other crabs, interannual variations in mean catch-per-tow of coarsehand lady crabs were large. In the years 1979, 1981, and 1984, only about a tenth as many crabs were collected per tow as in the years 1980, 1982, 1985, and 1986 (Fig. 7).

Size frequencies of coarsehand lady crabs (sexes not distinguished) peaked at 7cm (Fig. 8). Wenner and Wenner (1989) reported coarsehand lady crabs from North Carolina to Florida, in depths of 4–20m, with average carapace widths of only 3–4.5cm. Our data showed that in the inshore stratum (<27m), 69% of the crabs were >5cm.

Catches of coarsehand lady crabs were highest at night or twilight in all trawl surveys (Table 3), indicative of nocturnal or crepuscular activity.

According to regression analysis, only temperature was significantly correlated with abundance of coarsehand lady crabs caught by trawl (Table 5). The correlations were smaller than those of northern lady crabs, possibly reflecting the more even distribution of the coarsehand lady crab within its range.

Conclusion

The four most common crab species on the northwest Atlantic shelf have spatial and temporal distributions that are quite different. *Cancer* species occur at higher

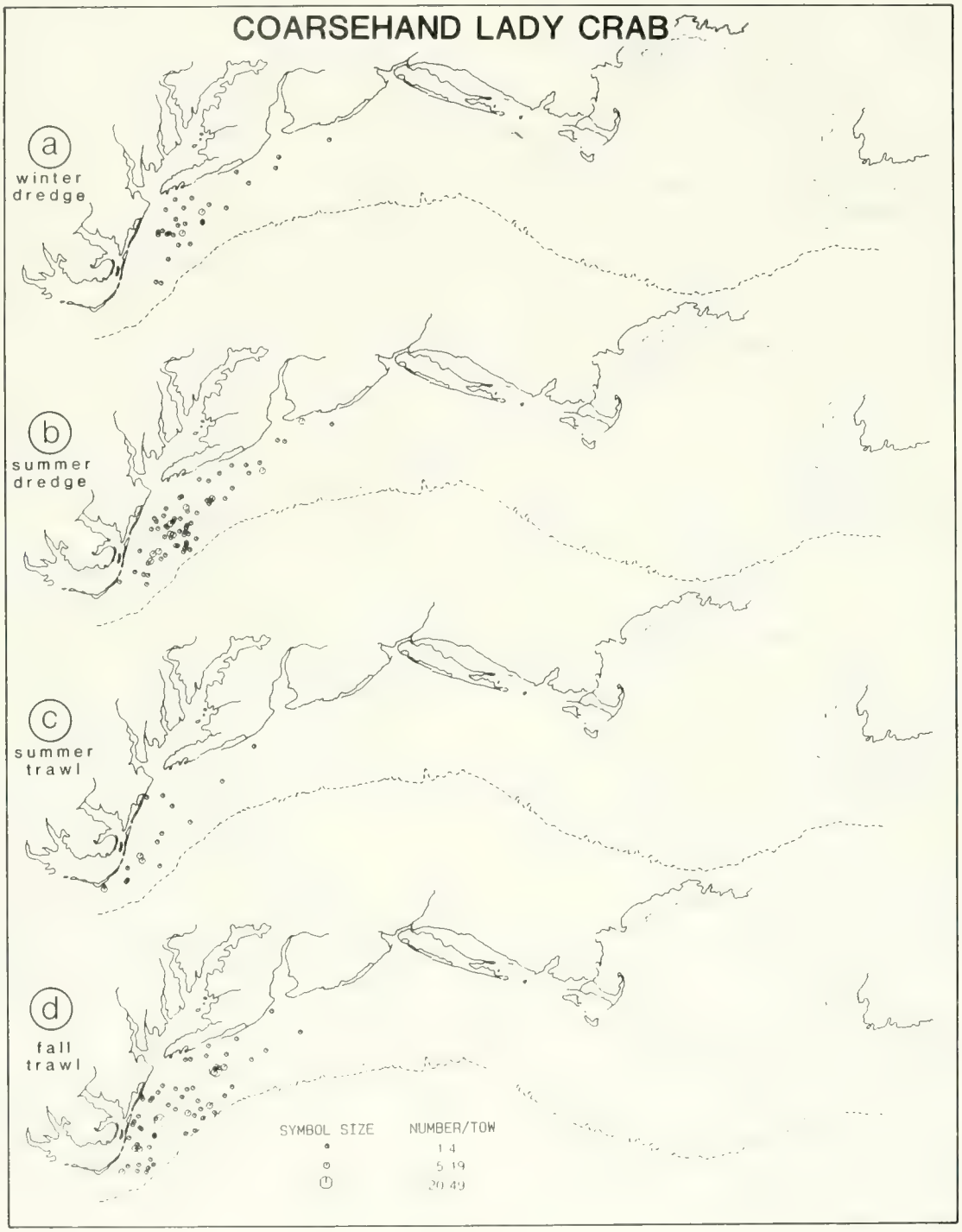

Figure 13
Coarsehand lady crab distribution, from winter dredge, summer dredge, summer trawl, and fall trawl surveys.

latitudes and lower temperatures than *Ovalipes* species. Rock and northern lady crabs are most abundant at inshore strata, but rock crabs are active throughout the year, whereas northern lady crabs are inactive in the winter. Jonah and coarsehand lady crabs are more sparsely distributed in the study area

and their abundances are seasonally consistent within each stratum. Depth or temperature, or their interaction, were significantly correlated with abundances of all four crab species.

Substantial gaps in the knowledge of these crabs remain. Temperature appears to affect distributions and migrations, but data to identify critical threshold temperatures are generally lacking. Besides depth and temperature, other factors such as food availability probably affect distribution, but are poorly known. The mean size at maturity for each species, the time of egg release, and locations of settlement and foods of juvenile crabs are scarcely known. Mortality rates of these crabs from fish predation are not known, and a comparison of the relative importance of the crabs with fishes as predators of benthic infaunal invertebrates has not been made.

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Life History and Ecology of Large Jacks in Undisturbed, Shallow, Oceanic Communities*

Anthony E. Sudekum
Department of Surgery, Stanford University Hospital
300 Pasteur Drive, Stanford, California 94305

James D. Parrish
Hawaii Cooperative Fishery Research Unit, U.S. Fish and Wildlife Service
2538 The Mall, University of Hawaii, Honolulu, Hawaii 96822

Richard L. Radtke
Biological Oceanography, School of Ocean and Earth Science and Technology
University of Hawaii, Honolulu, Hawaii 96822

Stephen Ralston
Tiburon Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
3150 Paradise Drive, Tiburon, California 94920

Abstract.–The large jack species *Caranx ignobilis* and *Caranx melampygus* were collected from the nearly pristine shallow waters of the atolls, reefs, and shoals of the Northwestern Hawaiian Islands. Both species were aged by counting daily otolith increments and validating frequency of otolith deposition by marking captive fish with tetracycline. Growth for each species was well described by a von Bertalanffy relationship. Measured growth of captive *C. melampygus* was also in agreement. Gravid fish of both species were found only in April–November; peak spawning season for both was about May–August. Reproduction began at ~350 mm SL (~2 years old) in *C. melampygus* and at ~600 mm SL (~3½ years old) in *C. ignobilis*. Fecundity of female *C. melampygus* varied approximately as the 1.7 power of body weight. Both species were >90% piscivorous, as judged from combined volume and number of prey and incidence of predation. Crustaceans and cephalopods comprised several percent of the diet of *C. ignobilis*; both groups were present but less important in *C. melampygus*. Both jack species ate gastropods in trace amounts. The overall diet of the two species showed moderate overlap: "Pianka's" index of overlap, $A_{yz} = 0.42$. The rate of food consumption for captive *C. melampygus* was used to estimate the respiratory metabolic coefficient, which in turn was used to estimate respiratory demands for all size-classes of both species. The von Bertalanffy model predicted growth energy, and reproductive energy was estimated from values of the gonadosomatic index. These energy terms were combined to calculate the food consumption required to sustain all size-classes appearing in local catch data. This distribution can be represented by a composite individual for each species consuming a little less than 50 kg/year (*C. melampygus*) and about 150 kg/year (*C. ignobilis*). Rough population estimates indicated that at one well-studied atoll, the two species populations combined may eat over 30,000 metric tons of prey per year. These results suggest a quantitatively important trophic role for these top-level carangid predators.

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Large jacks (family Carangidae) are widely distributed in tropical and subtropical waters and are highly prized in local fisheries wherever they occur. Where their populations have not been depleted by fishing, these large, active predators are often abundant, and they are probably important in the ecology of nearshore communities. In particular, *Caranx ignobilis* (Forskal) and *C. melampygus* (Cuvier and Valenciennes) are large carnivores that occur commonly throughout much of the tropical Indo-Pacific. These fast, wide-ranging species occupy the entire water column, but their habitats appear to be mostly demersal. They seem to maintain important ties with the demersal fish and benthic fauna of shallow coastal areas, islands, atolls, and isolated shoals.

In Hawaii, these two species are commonly the most abundant of the large, shallow-water, demersal jacks. Large jacks, and these *Caranx* species in particular, have long been important food and market fishes in Hawaii (Cobb 1905, Hamamoto 1928, Titcomb 1972). Heavy commercial and recreational fishing pressure has developed, especially in the last several decades (Gosline and Brock 1960, Ralston and Polovina 1982, Ralston 1984, Ralston and Kawamoto 1988, Hawaii DLNR 1989), and stocks in the main, inhabited islands are certainly considerably depressed (Shomura 1987).

Despite their widespread occurrence and importance in fisheries, the species biology and ecology of most jacks have been inadequately studied, and little information is available to guide decisions for fishery management. For species such as *C. ignobilis* and *C. melampygus*, which combine large size, high natural abundance, and aggressive feeding habits, the predatory effects on the demersal fauna might be expected to be significant. Therefore, study of the species biology and ecology of these jacks is important both for manage-

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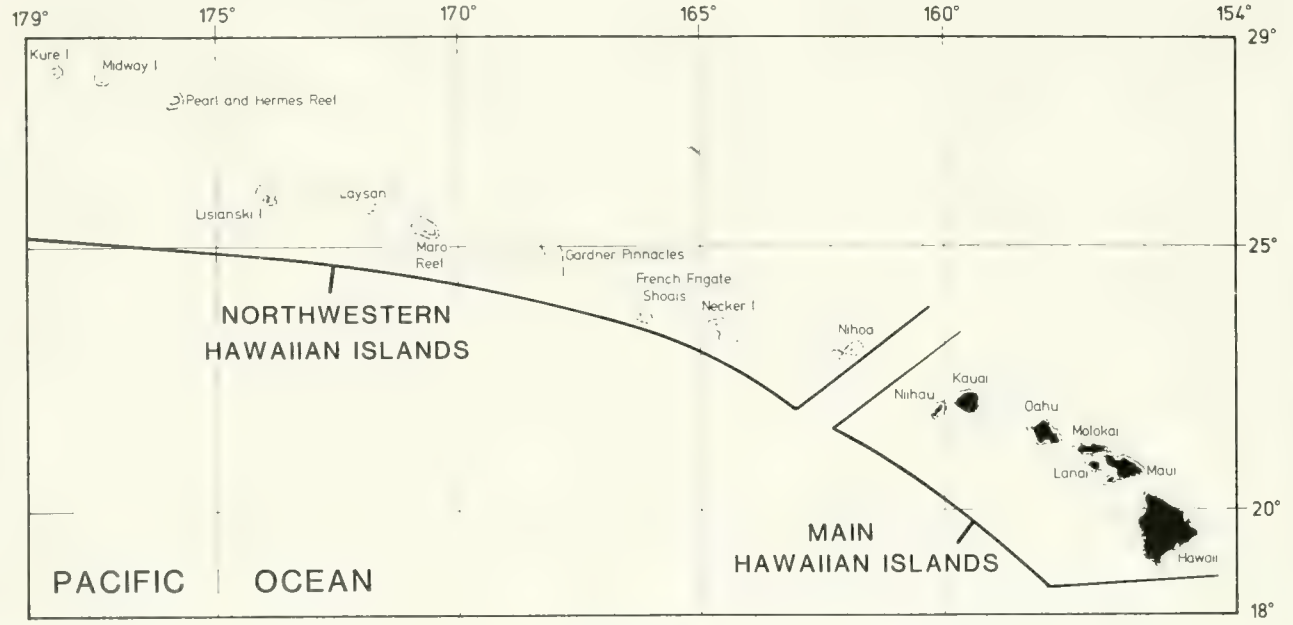

Figure 1
The Hawaiian archipelago. Nearly all specimens analyzed in this study were collected from the Northwestern Hawaiian Islands.

ment of their fisheries and for understanding the ecology of the communities in which they occur.

The uninhabited Northwestern Hawaiian Islands (NWHI) (Fig. 1) offered a particularly appropriate study area because of their size, isolation, and almost pristine biotic communities. Their ecology and natural resources were the subject of a 5-year, multi-agency study (Grigg and Pfund 1980, Grigg and Tanoue 1984), which included major trophic work on shallow-water communities by the Hawaii Cooperative Fishery Research Unit (e.g., DeCrosta et al. 1984, Sorden 1984, Parrish et al. 1985, Norris and Parrish 1988). The present study was done in conjunction with this larger program. Results from these relatively undisturbed carangid populations in the NWHI are also relevant for other populations of large jacks and for management of exploited jack populations.

Materials and methods

Collection information

Specimens of one or both species were collected from French Frigate Shoals (FFS), Maro Reef, Midway Islands, Pearl and Hermes Reef, Lisianski Island, and Necker Island (Fig. 1). Samples were obtained by a wide variety of methods, including handlining, trolling, casting, longlining, and spearing by divers using SCUBA. All jacks came from water less than 30 m deep. In atoll waters, they were taken both inside and outside the barrier reefs. Collections were made irregularly between September 1978 and March 1983, including all months of the year except February (*C. melampygus*) and February and December (*C. ignobilis*). A little over half of all specimens were taken in fall (September–November). Night collections were logistically difficult and largely unproductive. Therefore, there is a daytime bias in the sampling that may have influenced dietary results. The unpreserved fish were weighed whole, and the standard (SL), fork (FL), and total (TL) lengths were measured to the nearest millimeter. Guts of all specimens were injected with formalin in the field and/or frozen promptly. Data were taken on a total of 154 *C. melampygus* and 120 *C. ignobilis*.

Age and growth

For a selected group of specimens covering a wide range of sizes of both species, age was estimated by counting short-period increments of carbonate deposition in otoliths (Radtke 1987). The fish were decapitated along a boundary represented by the edge of the operculum. A sagittal cut was then made through the midline of the head and the cranial cavity exposed. The

Table 1

Relationships determined by regression among standard (SL), fork (FL), and total (TL) lengths in millimeters and whole wet body weight (W) in grams for *Caranx melampygus* and *Caranx ignobilis*.

Caranx melampygus			*Caranx ignobilis*		
Functional relationship	Square of correlation coefficient (r^2)	Sample size (n)	Functional relationship	Square of correlation coefficient (r^2)	Sample size (n)
$W = 2.86 \times 10^{-5} (SL)^{2.974}$	0.99	149	$W = 2.30 \times 10^{-5} (SL)^{2.977}$	0.98	118
SL = 0.929FL + 1.5	0.99	141	SL = 0.924FL + 6.0	0.99	107
SL = 0.878TL − 17.4	0.99	140	SL = 0.855TL − 17.5	0.98	107
TL = 1.052FL + 24.3	0.99	140	TL = 1.070FL + 35.7	0.99	107

sagittae were clearly evident in this dissection. Otoliths were removed from each side of the cranial cavity, cleaned, washed, stored in glycerol, then dried at 60°C for 24 hours, and weighed. Right and left otoliths were segregated.

Whole sagittae were embedded in epoxy casting resin and serially sectioned with a low-speed jewelers' saw. Sections 300 μm thick were attached to scanning electron microscope (SEM) viewing stubs with 5-min epoxy and polished with 0.3 μm alumina paste. The polished sections were etched for 1–20 minutes with 6% ethylene diamine tetraacetate (EDTA) with pH adjusted to 8 with sodium hydroxide. The otolith sections were washed in water, dried, coated with gold, and viewed in an SEM at various magnifications.

A sample of five right sagittae were sectioned in different planes as described by Radtke (1987) to determine that the optimum plane for enumerating increments was the transverse frontal plane. With this technique, we believe that no increments were lost in the chosen plane. Smallest increments were counted with the SEM on sections in this plane of the left sagittae of all specimens used for age determination. Increments were counted from sequential SEM images of the otolith surface, starting at the origin (center) and moving to the otolith margin at the rostrum (anterior). With this methodology, the area read for ageing was consistent for all individuals analyzed. On the assumption that one increment equals one day's growth (Pannella 1971 and 1974), the data were fitted to the von Bertalanffy growth equation (Fabens 1965).

A marking study using tetracycline was undertaken to validate the assumption of daily periodicity of otolith increments. Live carangids were collected from Kaneohe Bay, Hawaii by commercial fishermen using bait nets. Six juvenile *C. melampygus* (197–338 mm SL) and four juvenile *C. ignobilis* (113–225 mm SL) were acclimated for 1 month in a tank of flowing seawater 5.5 m in diameter by 0.6 m deep, exposed to natural sunlight. After 1 month, the fish were measured and given an intraperitoneal injection of 27.5 mg/kg wet body weight of oxytetracycline. To reduce trauma to the fish, they were not weighed at the time of the injections, but their weights were estimated from length-weight relationships derived from wild-caught fish (Table 1). The fish were fed *ad libitum* on a diet of raw herring until recapture, when they were sacrificed. Five *C. melampygus* were sampled after 55 days, the sixth *C. melampygus* and the four *C. ignobilis* after 137 days. Upon recapture, all fish were weighed and standard, fork, and total lengths were measured.

Sagittae from all experimental fish were removed, cleaned, dried, and mounted in clear casting resin. Sections were made both perpendicular and parallel to the rostral axis of the otolith. The sections counted were in a transverse frontal plane, much the same as those prepared for the SEM and as described by Radtke (1987). Sections were polished with 400-grit Carborundum wet-dry sandpaper, mounted on glass slides, and viewed at 300× under a binocular microscope with an ultraviolet light source. The number of increments between the fluorescent mark and the outside edge of the otolith was counted and compared with the number of days that the fish was alive after injection.

Reproduction

Sex ratio, spawning season, and size at first reproduction (SFR) were estimated for both species. Gonads were visually examined and classified as male, female, immature, or unknown. These classifications were based on the size, color, morphology, and texture of the gonadal tissue. Gonads from 70 *C. melampygus* and 10 *C. ignobilis* were removed, wet weighed to the nearest gram, and kept frozen for later, more detailed analysis.

Spawning season was estimated by visual examination of gonads and classification of the mature gonads as either developing or gravid (Kesteven 1960). Months were noted in which there was a significant increase in the number of gravid fish collected relative to the number of mature fish with developing gonads. Spawning season was also estimated by using the gonadosomatic index (GSI):

GSI =

(gonad wet weight/whole body wet weight) × 100.

The GSI for each mature individual was plotted against the date of capture. The spawning season was defined as the period of the year during which a significant proportion of the fish had high GSI values.

To determine the SFR, all fish taken during the spawning season were put into size-classes based on standard length (50 mm SL classes for *C. melampygus* and 100 mm classes for *C. ignobilis*). The number and percent of individuals with gravid gonads in each size-class was determined. As body size increased, at sexual maturity the percent of fish with gravid gonads rose sharply. The lower limit of the size-class in which 50% gravid gonads was reached was taken as the SFR. The SFR was transformed to an age at first reproduction by using the length-age relation from the von Bertalanffy growth equation.

Ovaries from gravid females captured during the peak of the spawning season were used to estimate fecundity, which is defined here as the estimated number of mature ova in the gonad of a spawning female at one time (Everhart and Youngs 1981). Three 2 g aliquots from various parts of each ovary were combined and placed in Gilson's fluid (Simpson 1951). This solution hardens and liberates the eggs and breaks down the ovarian tissue. The egg masses were left in this fluid for 2 weeks, then washed with water and the ovarian tissue removed. Subsamples were obtained by using van Dalsen's (1977) technique as modified slightly by Everson (1984). Each ovary sample was brought up to 500 mL with water and mixed with a magnetic stirrer. When a homogeneous mixture was obtained, three 5 mL aliquots were drawn. All ova more than 0.4 mm in diameter in each 5 mL subsample were counted using a binocular dissecting microscope. A fecundity estimate, F, was calculated from the formula

$$F = ((N_1 + N_2 + N_3)/3) \times (500/5) \times (G/S)$$

where N_1, N_2, N_3 = the number of mature ova in each subsample,
G = total gonad weight,
S = weight of the gonad sample placed in the Gilson's fluid.

Diet

Contents were removed from preserved guts and all prey identified to the lowest taxa possible. The number of individuals and volume of each taxon were noted, as well as the length, weight, and extent of digestion. Many fish in advanced states of digestion were identified by using reference collections of Hawaiian fish scales (Sylvester 1969) and skeletons. Whole prey lengths and volumes were approximated in many cases by comparison of the dimensions of recognizable parts with reference specimens of common Hawaiian reef fishes. The index of relative importance (IRI) was calculated, as defined by Pinkas et al. (1971),

IRI = (numerical % + volume %) × frequency %,

where, for each predator species,
numerical % = (number of individuals of one prey category divided by total number of prey individuals found in all the guts) × 100,
volume % = (volume of one prey category divided by total volume of all prey found in the guts) × 100,
frequency % = (number of guts containing prey of one category divided by total number of guts that contained any identifiable prey items) × 100.

A measure of dietary overlap between *C. melampygus* and *C. ignobilis* was provided by the index of overlap, A_{yz} (Pianka 1973). The value of the index varies from 1 when diets are identical with respect to proportional IRI composition to 0 when diets are distinct. We calculated the index using the formula

$$A_{yz} = \left(\sum_i p_{iy}\, p_{iz}\right) \Big/ \left(\sum_i p_{iy}^2 \sum_i p_{iz}^2\right)^{1/2},$$

where p_{iy} and p_{iz} are the proportions of the total IRI represented by the ith prey category for predator species y and predator species z, respectively.

The effect of individual predator size on the diet of *C. melampygus* was assessed by comparing the occurrence of prey items found in the guts of sexually immature and mature fish.

Energy budget and population consumption

Ingestion rates were measured in captivity. A group of six *C. melampygus* and a group of four *C. ignobilis* were held in separate sections of a tank of flowing seawater 5.5 m in diameter and 0.6 m deep. Standard, fork, and total lengths were measured for all fish, and then they were allowed to acclimate to the tank for 1 month while being fed raw herring at least once a day. Uneaten food was removed and the weight consumed was calculated for each feeding. Maximum feeding rates were estimated by feeding *ad libitum* at least three times daily during several intensive feeding periods that ranged between 4 and 10 consecutive days each. The fish used in this experiment were not the same individuals used in the tetracycline marking experiment.

Age-specific rations (rates of food consumption) of the two jack species in the wild and annual consumption by their total populations were estimated by using the measured ration in captivity for specimens of one size, together with results obtained by the preceding procedures for growth, reproductive output, and length-weight relationship. Data for the captive specimens were used in the basic energy budget model for fish (Mann 1965 and 1969, Parrish 1975) to obtain the respiratory metabolic rate, Q,

$$kC = Q + S + G$$

where k = ration assimilation coefficient, representing the fraction of the ingested ration available for utilization in metabolic processes,
C = ration, or rate of food consumption,
Q = rate of respiratory metabolism,
S = rate of production of reproductive material,
G = growth rate.

For the captive fish, ration (C) was measured. Growth (G) was both measured and estimated from the von Bertalanffy model. The value of $k = 0.8$ (Winberg 1956:209, Mann 1967 and 1969) was adopted. Since the fish were prereproductive, the reproductive term (S) was absent. The respiratory metabolic coefficient (α) was estimated from the relationship

$$Q = \alpha W^{\gamma},$$

using the calculated Q, the weight (W) of experimental fish, and $\gamma = 0.8$ as a reasonable approximation for most fishes (Winberg 1956:149, Mann 1965 and 1969, Paloheimo and Dickie 1965 and 1966). This coefficient was then used in the original model to calculate Q for fish of any weight, W. No experimental results were available to estimate α directly for *C. ignobilis*. In view of the other similarities with *C. melampygus* and the high probability of strong metabolic similarities, the value of α for *C. melampygus* was also used for *C. ignobilis*. The corresponding growth rate for any weight was derived from the von Bertalanffy model (computing age corresponding to weight from the model directly and evaluating the first derivative of the model at that weight). For fish larger than the SFR, the maximum observed GSI was used with the body weight to estimate the rate of production of reproductive material (S). With all three terms on the right side of the model computed, ration (C) was readily determined for fish of any size.

The size-frequency distribution of the wild population of each species was estimated by pooling length and weight data for all specimens collected in this study with data compiled by the Hawaii Division of Aquatic Resources and the National Marine Fisheries Service: in total, some 253 specimens of *C. melampygus* and 802 of *C. ignobilis*. Weight-class increments of 200 g were used for *C. melampygus* and 500 g for *C. ignobilis*. The fraction in each size-class was multiplied by the appropriate computed ration, and the results were summed to estimate an individual ration representative of the population as a whole. This ration of the representative individual, multiplied by the population size for any area, provides an estimate of consumption rate by the entire population.

Population sizes for both species were estimated for one of the the major study areas, French Frigate Shoals (FFS), using two methods. First, sightings of the species made during 56 visual underwater transect censuses in a variety of shallow-water habitats were pooled. For a crude population estimate, for such wide-ranging species, the distribution of these censuses over the various habitat types was taken as representative of all the habitats occupied by these fishes. Each sighting was expressed as the number of fish seen per unit area. Estimates of the total submerged area of FFS of less than about 20 m depth (the apparent prime depth range of these species locally) were based on data from Atkinson and Grigg (1984), Agegian (1985), and J.J. Polovina (NMFS Honolulu Lab., Southwest Fish. Sci. Cent., pers. commun.). The product of this area and the population density estimates from the visual census provided rough estimates of the total populations of both jack species at FFS.

A second population estimate was based on the assumption that the density of the almost unexploited jack populations at FFS must be higher than the

population density indicated by the highest catches on record for other parts of the archipelago where fishing is significant. Data from the highest catches reported (Cobb 1905) were used directly where species were identified in the catch statistics. Where species were reported pooled in the statistics, they were separated by making the assumption that both species of interest occurred as the same percentage of all shallow-water, demersal, large jacks in 1900—the year in which the data of Cobb (1905) were collected—as in 1981–86 (when catch data were available by species). The catches of the two species in 1900, thus reconstructed, were converted to densities using the summed area (Agegian 1985) within these species' habitat depth range around the main, inhabited Hawaiian islands where the 1900 statistics were obtained. These densities provide a lower limit to estimates of the FFS population densities.

The products of jack population estimates with the respective rations of the representative individual for each species produced estimates for total population consumption (or predation pressure), including all prey consumed. The predation pressure on each prey category was obtained by multiplying these total consumptions by the volume percent (as a decimal fraction) for that prey category.

Results

Age and growth

The relationship between whole wet body weight (W) and standard length (SL) was described for both species by performing a log-linear power function regression on these two variables (Table 1). For both species, weight is approximately a cubic function of standard length, indicating nearly isometric growth. The similarity in parameter estimates (Table 1) is consistent with the morphological similarity of these two species. Linear regressions were performed to permit conversion between standard, fork, and total lengths (Table 1).

Otolith growth increments from 14 *C. melampygus* and 10 *C. ignobilis* (Table 2) were counted with the aid of SEM (Fig. 2) to estimate age (Appendix A). Assuming that increments were deposited daily, the data were fitted to the von Bertalanffy growth equation (Fig. 3) for fish SL, 1_t (in millimeters), as a function of age, t (in years),

Table 2

Parameters of the von Bertalanffy growth model for *Caranx melampygus* and *Caranx ignobilis* and summary of data used for the regressions.

	Caranx melampygus	*Caranx ignobilis*
L_∞ (asymptotic SL)	897 mm	1838 mm
W_∞* (asymptotic whole wet weight)	17,313 g	120,139 g
K	0.233/year	0.111/year
t_0	−0.044 year	0.097 year
r^2 [correlation coefficient]^2	0.99	0.99
n (sample size)	14	10
Range of SL used	122–660 mm	106–1180 mm
Range of estimated ages	0.51–5.90 year	0.75–9.27 year

*Based on standard length-weight relationships from Table 1.

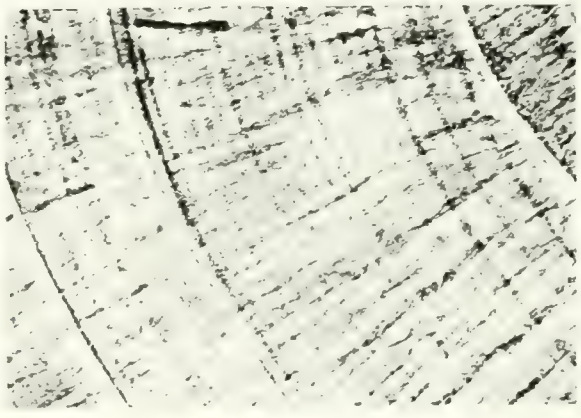

Figure 2

Scanning electron micrograph of a sagitta from *Caranx melampygus*.

$$1_t = L_\infty (1 - e^{-K(t-t_0)}).$$

The estimates for the parameters are shown in Table 2.

The accretion rate of otolith growth increments was measured in *C. melampygus* using six tetracycline-marked animals, held 55 days after injection. A discrete fluorescent line was discernible in all six subjects (Fig. 4), although marginal increments (developed peripheral to the line) were evident in only five. Three thin replicate sections were made from the sagittae of each, and marginal increments were enumerated, although one of the five specimens produced only two satisfactory preparations.

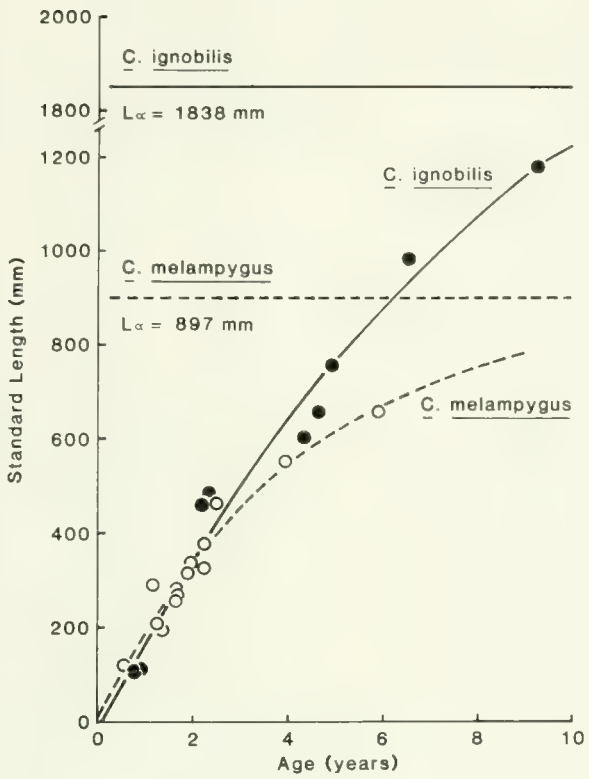

Figure 3

Growth data and von Bertalanffy growth curves derived for *Caranx melampygus* and *Caranx ignobilis*. Age was estimated by counting daily growth increments of otoliths. (See Table 2 for details.)

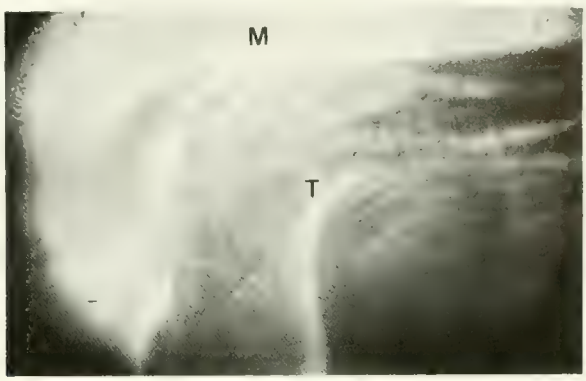

Figure 4

Ultraviolet-white light double-exposure micrograph of a section of sagitta from *Caranx melampygus*, marked for growth validation. The fish specimen had been injected with tetracycline 55 days before sacrifice. The fluorescent tetracycline mark (T) is visible as a light band inside the otolith margin (M).

The 14 counts yielded a pooled mean of 51.6 marginal increments (range 47–62, SD 4.31) and a 95% confidence interval of 49.1–54.1 increments. One-way analysis of variance, however, showed that significant differences existed among the five fish in mean increment count (F 4.61, df 4, 9, P 0.027). Furthermore, variation in marginal increment deposition within specimens (s^2 8.80) was comparable to that between specimens (s^2 10.59). When mean counts of the five individual fish were compared, the 95% confidence interval for the population mean was 47.0–56.1 marginal increments. The number of days since injection (55) falls within this interval, and in general the marginal counts are reasonably close to this number.

During the maximum feeding-rate experiment, the six specimens of *C. melampygus* increased from an average standard length of 174mm (range 166–185 mm) to 239mm (range 225–252mm) over a period of 161 days. This represents an average growth rate of 0.40mm/day. An instantaneous growth rate of 0.45 mm/day (1.02g/day) was calculated for "wild" fish within the same size range by using the von Bertalanffy growth curve.

Reproduction

Sex was determined in 119 specimens of *C. melampygus* and 110 specimens of *C. ignobilis*. In both species, the sex ratio of the samples, M:F, was slightly skewed toward females: 1:1.48 for *C. melampygus* (χ^2 4.45, df 1, P 0.04) and 1:1.39 for *C. ignobilis* (χ^2 2.95, df 1, P 0.08).

Using morphological criteria, gonads from 152 *C. melampygus* and 124 *C. ignobilis* were visually classified into one of three reproductive stages (immature, developing, or gravid). To test the accuracy of this visual technique, gonadosomatic indices from 62 *C. melampygus* were compared with the reproductive stages assigned visually for each fish. A two-way factorial analysis of variance, with stage (immature, developing, or gravid) and sex (male or female) as classification variables and log-transformed GSI as the dependent variable, showed that stage (F 44.34, df 2, 52, $P<0.0001$), but not sex (F 0.95, df 1, 52, P 0.334) affected gonadosomatic index. The interaction term was insignificant (F 1.69, df 2, 52, P 0.194). Mean values of the untransformed GSI's for the three stages of reproductive condition were 0.16%, 0.42%, and 4.54%, respectively. Sidak t-tests (SAS 1985) revealed that all three means were significantly different from one another. Thus, the two methods of establishing reproductive condition show a high degree of concord-

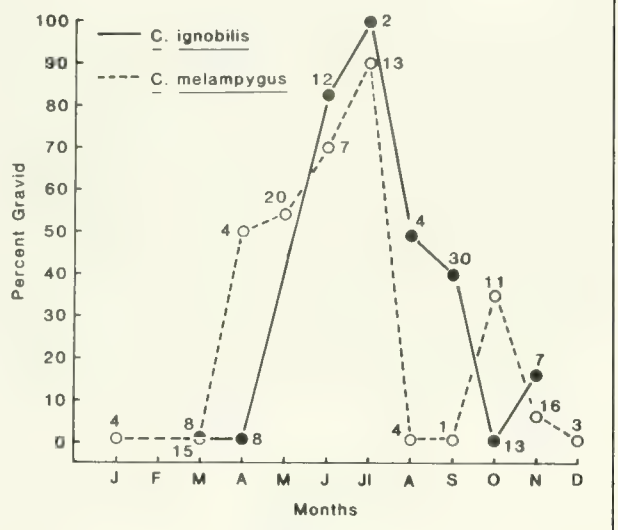

Figure 5

Percent of *Caranx melampygus* and *Caranx ignobilis* found gravid for each monthly sample available (as established by visual gonad classification). Numbers on the figure indicate individual sample sizes. Total sample sizes were 98 *C. melampygus*, all >350 mm SL, and 84 *C. ignobilis*, all >600 mm SL.

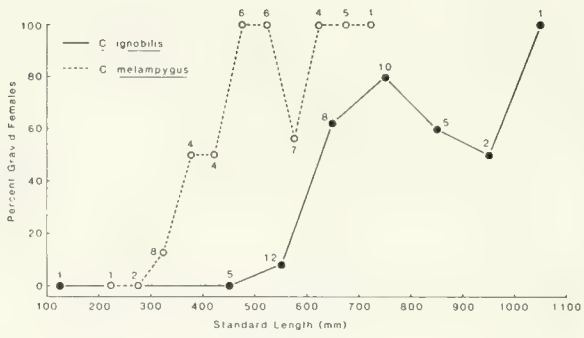

Figure 6

Size at first reproduction for female *Caranx melampygus* and *Caranx ignobilis*. Percent of sampled females found gravid (by visual gonad classification) in each size-class is plotted against standard length. Only fish sampled during summer spawning season are included. Numbers on the figure indicate individual sample sizes. Total sample sizes were 48 *C. melampygus* and 43 *C. ignobilis*.

ance. Visual gonad stage was the variable we used most often for determining spawning season and SFR.

Of 98 mature *C. melampygus* (>350 mm SL) compared by visual gonad classification, gravid individuals were found from April to November (Fig. 5). In May, June, and July more than half the individuals were gravid. Results from April, August, and September are questionable because sample sizes were small. The GSI's were also plotted against the month of capture to determine spawning season for *C. melampygus*, with consistent results. Again June and July were the peak months, but there were no gonad samples from which GSI's could be calculated in April or May. A peak in reproductive condition was also visually observed in gonads of mature (>600 mm SL) *C. ignobilis* in summer (Fig. 5). No animals of mature age were caught in December, January, or February, but only 1 of the 36 taken from October to April was gravid.

Among 48 female *C. melampygus* caught during spawning season (April to October), first reproduction (based on visual gonad classification) appeared to occur between the 325 mm and 375 mm length-classes. In this size range, the percent of gravid individuals increased sharply from 12% to 50%, and at least 50% of all larger females were gravid during these months (Fig. 6). For 43 female *C. ignobilis* caught from May to October, there was a sharp increase from 8% to 62% gravid between the 550 mm and 650 mm length-classes (Fig. 6), and all larger length-classes had a higher incidence of gravid females. Thus, it appears that female *C. melampygus* reach sexual maturity at about 350 mm SL, and female *C. ignobilis* at about 600 mm SL.

Fecundity was estimated for *C. melampygus* from ovaries of 11 gravid females caught in July. The estimated fecundity ranged from 49,700 mature ova for a fish of 760 g (328 mm SL) to 4,270,000 for one of 6490 g (640 mm SL) (Appendix B). A log-linear power function regression was performed in which fecundity, F, in number of eggs, was compared with total wet body weight, W, in grams, and SL, in millimeters. The regression equations are:

$$F = 0.923\ W^{1.694}, \qquad (r^2\ 0.84),$$

$$F = 2.286 \times 10^{-9}\ (SL)^{5.359}, \qquad (r^2\ 0.80).$$

Diet

Of 118 guts of *C. ignobilis* examined, 68.6% contained identifiable prey items, which were subjected to qualitative and quantitative analysis (Table 3). Of the *C. ignobilis* guts with identifiable prey items, 80.3% contained the remains of fishes. Parrotfish (Scaridae) were the most important identified family of fish in the diet, occurring in 13.6% of the guts that contained prey. Carangids, most notably the opelu *Decapterus macarellus*, were identified in 8.6% of the guts, and wrasses (Labridae) and bigeyes (Priacanthidae) each occurred in 6.2%. Eels (Anguilliformes: Muraenidae, Congridae,

Table 3

Summary of stomach content analysis for *Caranx ignobilis* based on 81 specimens containing prey identifiable to some taxonomic level. At the highest systematic level of analysis, unidentified fish were included in the total number of prey individuals. (In addition, only numerical and frequency percents were calculated for unidentified fish, as shown within parentheses.) Unidentified fish were not included in the totals used to calculate volume percent nor in any analysis at lower systematic levels. Percentages for a few identifiable species appear within brackets [ ]; no IRI was calculated at this level. All values not underlined or enclosed were used together as a single level for analysis.

Prey item	Numerical %	Volume %	Frequency %	% of summed IRI
Fish	69.1	73.1	80.3	90.2
Scaridae	13.4	13.4	13.6	23.0
Carangidae	5.2	4.5	8.6	5.3
Decapterus macarellus	[2.2]	[2.3]	[3.7]	
Labridae	3.7	15.6	6.2	7.5
Priacanthidae	3.7	6.8	6.2	4.1
Muraenidae	6.0	4.9	6.2	4.3
Congridae	6.0	5.1	6.2	4.3
Unidentified eels	4.5	4.7	4.9	2.9
Mullidae	2.2	8.6	2.5	1.7
Parupeneus cyclostomus	[0.8]	[8.2]	[1.2]	
Pomacentridae	3.0	0.9	3.7	0.9
Ostraciidae	3.0	1.7	4.9	1.4
Monacanthidae	5.2	0.9	2.5	1.0
Acanthuridae	2.2	2.6	1.2	0.4
Holocentridae	0.8	2.9	1.2	0.3
Ophidiidae (*Brotula multibarbata*)	0.8	0.5	1.2	0.1
Unidentified fish	(24.2)	—	(44.4)	—
Crustaceans	12.9	11.0	17.3	3.3
Palinurid lobsters	3.0	10.5	3.7	3.2
Unidentified crustaceans (incl. 1 portunid crab)	14.2	0.6	13.6	12.6
Cephalopods	17.4	15.9	24.7	6.5
Squid	10.5	2.8	9.9	8.3
Octopus	11.2	12.5	12.4	18.4
Unidentified cephalopods	1.5	0.6	2.5	0.3
Gastropods (*Bittium parcum*)	0.6	—	1.2	<0.05

and unidentified) were found in 14.8% of the guts, cephalopods in 24.7%, and crustaceans (including lobsters, crabs, and shrimp) in 17.3%.

Of 147 guts of *C. melampygus* examined, 85.0% contained identifiable prey items (Table 4), and 96.0% of these contained the remains of fish. The wrasses (Labridae), goatfish (Mullidae), filefish (Monacanthidae), damselfish (Pomacentridae), parrotfish (Scaridae), and bigeyes (Priacanthidae) were the most important families of fishes in the diet of *C. melampygus*. Eels and cephalopods made negligible contributions. Crustaceans of many diverse groups were found in 19.2% of the guts with identifiable prey items, but they accounted for less than 1% of total prey volume. Palinurid lobsters were absent.

Comparison of the diets of the two length categories of *C. melampygus* showed only one significant difference. Crustaceans were found in 17 of 42 guts from fish of the smaller length category (<350 mm SL), but in only 7 of 107 guts from the larger length category (>350 mm SL). This indicates a statistically significant (χ^2 21.5, df 1, $P<0.001$) change in the diet of *C. melampygus* with size.

The Pianka (1973) index of overlap, used to measure the degree of similarity in the diets of the two carangids, was calculated from the proportional IRI representation (% of summed IRI) for each prey group found in the two species. The value of A_{yz} was 0.42.

Maximum feeding rates were determined for six captive juvenile *C. melampygus*. These fish started at a mean weight of 124.5 g, and during the course of the

Table 4

Summary of stomach content analysis for *Caranx melampygus* based on 125 specimens containing prey identifiable to some taxonomic level. At the highest systematic level of analysis, unidentified fish were included in the total number of prey individuals. (In addition, only numerical and frequency percents were calculated for unidentified fish, as shown within parentheses.) Unidentified fish were not included in the totals used to calculate volume percent. No unidentified animals from any major taxonomic group were used in any analysis at lower systematic levels. Percentages for some identifiable genera and species appear within brackets [ ]; no IRI was calculated at this level. All values not underlined or enclosed (except Caridea) were used together as a single level for analysis.

	Numerical %	Volume %	Frequency %	% of summed IRI
Fish	85.4	98.7	96.0	98.66
Labridae	18.1	13.0	23.2	36.4
Bodianus bilunulatus	[0.5]	[1.0]	[0.8]	
Thalassoma spp.	[3.8]	[2.8]	[4.8]	
Xyrichtys spp.	[1.9]	[1.7]	[1.6]	
Mullidae	7.1	17.7	12.0	15.0
Parupeneus multifasciatus	[1.9]	[8.0]	[3.2]	
P. cyclostomus	[0.5]	[3.5]	[0.8]	
Monacanthidae (*Pervagor* spp.)	13.3	7.4	12.0	12.5
Scaridae	6.2	19.0	8.0	10.2
Pomacentridae	7.1	9.4	10.4	8.7
Stegastes fasciolatus	[1.0]	[0.7]	[1.6]	
Chromis spp.	[2.4]	[5.0]	[2.4]	
Priacanthidae	5.2	16.0	6.4	6.8
Acanthuridae	2.9	6.7	4.0	1.9
Acanthurus nigroris	[0.5]	[4.9]	[0.8]	
Naso unicornis	[1.0]	[0.4]	[0.8]	
Synodontidae	2.9	2.0	4.8	1.2
Holocentridae	2.9	1.2	3.2	0.7
Flammeo sammara	[0.5]	[0.5]	[0.8]	
Belonidae	1.0	3.7	1.6	0.4
Kyphosidae	1.4	0.4	2.4	0.2
Pomacanthidae (*Centropyge potteri*)	1.0	0.8	1.6	0.15
Blenniidae	3.3	0.1	0.8	0.14
Ophichthidae	1.0	0.2	1.6	0.1
Muraenidae	0.5	0.5	0.8	0.04
Unidentified eels	0.5	0.2	0.8	0.03
Gobiidae	1.0	—	0.8	>0.04
Tetraodontidae	1.0	0.1	0.8	0.04
Scorpaenidae	0.5	0.2	0.8	0.03
Bothidae	0.5	—	0.8	>0.02
Unidentified flatfish	0.5	0.1	0.8	0.02
Unidentified fish	(34.8)	—	(44.0)	—
Crustaceans	11.2	0.9	19.2	1.3
Shrimp	9.0	0.4	9.6	4.6
Caridea (incl. *Alpheus, Saron* and *Rhynchocinetes* spp.)	2.9	0.14	4.8	
Crabs (incl. Portunidae and other Brachyura)	1.9	0.14	3.2	0.3
Stomatopods	2.4	0.14	3.2	0.4
Pseudosquilla ciliata	[1.4]	[0.06]	[1.6]	
Pseudosquilla oculata	[1.0]	[0.08]	[1.6]	
Isopods	0.5	—	0.8	>0.02
Cephalopods	0.6	0.4	1.6	0.01
Octopus	0.5	0.4	0.8	0.04
Gastropods (incl. *Bittium impendens, Vitricithna marmorata,* and *Modulus tectum*)	2.8	–	2.4	>0.04

161-day experiment, grew to a mean weight of 302.5g. All fish survived and appeared healthy throughout the course of the feeding experiment. Four intensive feeding periods of 6, 6, 4, and 5 days duration resulted in an average daily food consumption rate of 0.084g food per gram of fish. Three *C. ignobilis* specimens of about 500g each were used in a similar experiment. Three intensive feeding periods with these fish resulted in an average daily food consumption rate of about 0.05g food per gram of fish. However, this estimate is probably low because these experimental fish seemed to be in poor health during confinement.

Energy budget and population consumption

Based on the captive feeding experiments with *C. melampygus*, an estimate of $\alpha = 0.19 g^{0.2}$/day (at about 24°C) was derived and used for all energy budget calculations for both species. Estimates of all major components of the energy budget were calculated for the 38 weight-classes of *C. melampygus* (ranging from 200 to 10,000g) and the 71 weight-classes of *C. ignobilis* (ranging from 500 to 41,000g) represented in the size-frequency database. Table 5 contains selected

Table 5

Computed major components of an estimated energy budget for *Caranx melampygus* and *Caranx ignobilis* in the Northwestern Hawaiian Islands. Values are selected for various sizes within the full range of the size distribution (26 additional size-classes for *C. melampygus* and 55 for *C. ignobilis* are not shown). All energy rates are expressed in equivalent grams of fish tissue.

1 Weight class (g)	2 SL (mm)	3 Age (yr)	4 Growth rate, G (g/day)	5 Respiratory metabolic rate, Q (g/day)	6 Reproductive production rate, S (g/day)	7 Individual ration, C (g/day)	8 Fraction of population	9 Proportional ration of weight class* (g/year)
				Caranx melampygus				
200	200	1.05	1.29	13.17	0	18.08	0.057	375
1000	344	2.06	3.01	47.72	0	63.42	0.053	1223
1200	366	2.23	3.26	55.22	0.33	73.52	0.041	1091
2000	434	2.83	4.01	83.09	0.55	109.57	0.024	975
3000	498	3.47	4.56	114.93	0.82	150.39	0.016	892
4000	548	4.05	4.85	144.68	1.09	188.28	0.041	2794
5000	591	4.61	4.97	172.95	1.37	224.12	0.0081	665
6000	628	5.16	4.97	200.11	1.64	258.40	0.0041	383
7000	662	5.71	4.86	226.38	1.92	291.45	0.0041	432
8200	698	6.40	4.63	256.92	2.25	329.75	0.012	1468
9000	720	6.89	4.43	276.79	2.46	354.60	0.0041	526
10000	746	7.53	4.12	301.13	2.74	384.98	0.0041	571
Total (including weight classes not shown) = ration of individual representative of population =								47,815
				Caranx ignobilis				
1000	367	2.10	3.82	47.72	0	64.44	0.019	447
2000	458	2.68	5.75	83.09	0	111.06	0.037	1490
3000	521	3.10	7.24	114.93	0	152.72	0.058	3250
4000	571	3.45	8.47	144.68	0	191.44	0.018	1240
5000	613	3.75	9.53	172.95	1.37	229.82	0.014	1169
6000	650	4.03	10.47	200.11	1.64	265.29	0.011	1104
7000	682	4.28	11.31	226.38	1.92	299.51	0.024	2632
8000	712	4.51	12.07	251.90	2.19	332.70	0.032	3848
9000	739	4.73	12.76	276.79	2.46	365.02	0.030	4053
10000	764	4.94	13.40	301.13	2.74	396.59	0.027	3853
15000	870	5.87	15.93	416.51	4.11	545.69	0.021	4291
20000	953	6.69	17.71	524.30	5.48	684.35	0.011	2849
25000	1024	7.43	18.98	626.77	6.85	815.74	0.011	3396
30000	1085	8.14	19.87	725.19	8.22	941.60	0.0025	871
35000	1140	8.81	20.47	820.37	9.59	1063.03	0.0013	492
41000	1198	9.61	20.87	931.07	11.23	1203.97	0.0013	557
Total (including weight classes not shown) = ration of individual representative of population =								150,686

*Product of Columns 7 and 8, adjusted to annual basis.

Table 6

Annual consumption (ration) of entire estimated populations of *Caranx melampygus* and *C. ignobilis* at French Frigate Shoals (FFS) and predation on major prey categories.

Estimated total population at FFS	Ration of individual representative of population* (kg/yr)	Breakdown by prey category** Prey category	Volume % (from Tables 3 and 4)	Consumption of prey category (t/yr)	Total consumption by population (t/yr)
Caranx melampygus					
230,000	47.82				11,000
		Fish	98.7	10,854	
		Crustaceans	0.9	99	
		Cephalopods	0.4	44	
Caranx ignobilis					
130,000	150.69				19,600
		Fish	73.1	14,320	
		Crustaceans	11.0	2,155	
		Cephalopods	15.9	3,115	
Both species combined					
360,000					30,600
		Fish		25,174	
		Crustacens		2,254	
		Cephalopods		3,159	

* From Table 5

** Volume percent for gastropod prey was not measured; amounts were negligible compared with the other three categories.

values covering the full range of sizes, with energy rate terms expressed in fish tissue gram equivalents. Age and standard length were computed from the von Bertalanffy model, and energy components were calculated as described in the Methods section. Entries within a row in Columns 1–7 are all raw, unweighted values for an individual of a particular weight-class. Thus, Column 7 contains the estimated ration of a weight-class. In Column 9, this value is weighted by the fraction (Column 8) which that weight-class contributes to the total population. Thus, for *C. melampygus* the sum of all 38 "proportional ration" values such as the examples in Column 9 constitutes the ration of a hypothetical individual representative of the entire population, i.e., 47.82kg/year of prey. Similarly, for *C. ignobilis* the sum of all 71 "proportional ration" values provides the annual ration of such a representative individual, i.e., 150.69kg/year.

The best estimates of species populations for FFS that our census data permit are about 230,000 *C. melampygus* and 130,000 *C. ignobilis* (Table 6). Combined with the estimate of annual ration of the representative individual of each species, these values produce estimates of total annual consumption of about 11,000 metric tons (t)/year by *C. melampygus* (about 22 t/year per km^2 of prime habitat), and about 19,600 t/year by *C. ignobilis* (about 39.2 t/year per km^2). Table 6 shows the annual amount eaten of each major prey category, based on results in Tables 3 and 4.

Discussion

Age and growth

Length-weight data for these species have been previously reported. Seki (1986a) reported a power function regression based on 124 *C. ignobilis* specimens caught in the Northwestern Hawaiian Islands, ranging in FL from 207 to 1330 mm. Applying the FL–SL relationship of Table 1 to his result produced the expression,

$$W = 3.44 \times 10^{-5} (SL - 6.0)^{2.913}.$$

Over the range of sizes collected in both studies, predictions of W from this relationship and that of Table 1 (based on 118 NWHI specimens) agree within about 7% at worst, and for a large majority of the specimens they agree within 2–5%. Their predictions are most divergent (over 8.5%) as L_∞ is approached.

Seki (1986b) also reported an expression for FL versus weight based on only 24 specimens of *C. melampygus*, 93–710mm FL. Applying the FL–SL relation of Table 1 to this result produced the expression,

$$W = 3.0053 \times 10^{-5} (SL - 1.5)^{2.941}.$$

The agreement between predictions of this expression and those of Table 1 (based on 149 NWHI specimens)

is much poorer. Over the range collected in both studies, the relationship from Seki predicts W values 14.5–17% lower than our estimates; near L_∞, the difference is almost 18%. The larger difference compared with that for *C. ignobilis* may be due to the small sample size for one *C. melampygus* regression.

Williams (1965) also fitted a length-weight expression based on 75 *C. melampygus* specimens from east Africa. Converted to common units (SL in millimeters, W in grams), his relationship is

$$W = 1.4173 \times 10^{-5} SL^{3.066}.$$

Over the range of sizes occurring in both studies, this expression predicts weights 10–17% lower than ours and closer to those of Seki (1986b). Near L_∞ it is within 8% of our estimates, and for our smallest specimens its estimates are about 27% lower. The large differences between predictions of Williams' model and ours may reflect a difference in body proportions or in large-scale "condition factor" between this species in the NWHI and east Africa. Or the result may simply be an artifact of sampling. Williams (1965) commented that in his sample, males were probably larger on average and more variable in weight than females. The ratio of males to females was much larger in his sample than in ours.

Uchiyama et al. (1984) fitted length-weight data for *Seriola dumerili* and *Pseudocaranx dentex* from the NWHI to power functions. For all four of these large, closely related species, the data fit a power function model well and the parameter values are similar.

Uchiyama and Tagami (1984) reported a preliminary von Bertalanffy growth equation for *Seriola dumerili* based on counts of daily otolith increments up to about 2 years of age (well below the inflection point of the von Bertalanffy weight curve). These results show a faster initial increase in size early in life in *S. dumerili* than in either *Caranx* species. The K values for both *Caranx* species fall well within the range of common values for many large fishes.

For both *Caranx* species, our counts of otolith growth increments made with an SEM gave estimates of age that could be fitted well to the von Bertalanffy age-length model. The daily nature of increment deposition was partly validated for *C. melampygus* by the tetracycline marking experiment. Caution must be used in extrapolating the one-to-one correspondence to fish larger than those used in the validation experiment. Recent work has shown that growth increments in the otoliths of older fish may be deposited at intervals greater than one day (Pannella 1971, Wild and Foreman 1980, Ralston and Miyamoto 1983). If so, age would be underestimated and growth rate would be overestimated.

The close agreement between the growth rate measured for captive *C. melampygus* fed *ad libitum* and the natural rate estimated from the von Bertalanffy growth curve may be fortuitous. There are a number of aspects of the captive situation that might be expected to create disparity between these results. Even though the fish were fed at least daily to satiation, the confined tank environment and human disturbance may have affected their behavior or health and slowed their growth. These fish are wide-ranging active predators, and the laboratory tank provides an unnatural environment for feeding and metabolism. A limitation of the captive feeding study was that only young, fast-growing, sexually immature specimens were available. It is not clear that the growth pattern or metabolic parameters estimated from these experiments are fully applicable over the life span of the fish. Relative growth and ingestion rates are high at younger ages, and otolith ring deposition is more likely to be daily. It would be useful, but technically difficult, to perform these experiments with large adults.

The von Bertalanffy relationship obtained for *C. ignobilis* predicts a value of $SL_\infty = 1838$ mm, and (by use of our length-weight regression) $W_\infty = 120.14$ kg. By comparison, the largest *C. ignobilis* specimens reported caught in Hawaii (with length estimates based on our regression) are 86.71 kg (1648 mm), 81.49 kg (1613 mm), and two specimens of 68.10 kg reported as measuring about 1524 mm and 1626 mm FL, respectively (about 1417 mm and 1512 mm SL, on the basis of our regressions) (Chuck Johnston, Editor, Hawaii Fishing News, Honolulu, pers. commun.). All these reports are from the main, inhabited Hawaiian islands and reflect recent conditions, following several decades of heavy fishing pressure on the species. Larger specimens may occur in the relatively unfished NWHI, where stocks are in near virgin condition and sampling has been sparse.

For *C. melampygus*, the predicted $SL_\infty = 897$ mm and $W_\infty = 17.31$ kg. Catch records from the fishery are not well documented. However, there are reliable reports of a *C. melampygus* caught on Oahu that weighed just over 19 kg and one caught on Lanai that weighed about 13.6 kg (Peter Dunn-Rankin, Univ. Hawaii, Honolulu, pers. commun.). The largest specimen for which we found documented record was one of our own: SL = 760 mm, W = 10.00 kg. From sizable collections by the Hawaii Division of Aquatic Resources and by the National Marine Fisheries Service, the largest specimens reported (with length estimates based on our regression) were 8.20 kg (698 mm) and 6.40 kg (642 mm), respectively. For both these jack species, the values of L_∞ and W_∞ derived from our size-age data are close to or somewhat greater than reported values.

Reproduction

The sex ratios for both species were skewed slightly toward females. The deviation from unity was not highly significant, and the difference may be merely a sampling artifact. Off the coast of east Africa, Williams (1965) reported overall sex ratios significantly biased toward males for both *C. melampygus* (M:F 1.68:1, *N* 78) and *C. ignobilis* (M:F 2.01:1, *N* 323). Males also predominated in an earlier series of collections there (Williams 1956). Off Zanzibar Island (east Africa) during the summer spawning season, he reported encountering shoals of "ripe and running" *C. ignobilis* composed almost entirely of males. He also sampled shoals where only females were caught and suggested that the sexes segregate in the prespawning period. Our catch data indicate that disproportionate numbers of gravid females were taken from large schools during summer. This behavior suggests that spawning by *C. ignobilis* is not a random process, but is coordinated in space and time. Whether or not large numbers of males and females aggregate to spawn is unknown, but seems likely.

Based on the data in Figure 5, it appears that both species spawn primarily in summer. However, the paucity of quantitative gonad data (e.g., GSI's) makes it difficult to present a complete picture of the annual reproductive cycle for either species. A review of the spawning patterns of Hawaiian fishes by Walsh (1987) suggested that most Hawaiian reef fishes spawn primarily during summer.

Based on the condition of gonads examined in the field, Williams (1956, 1965) concluded that spawning of *C. ignobilis* off east Africa (1°S–10°S lat.) occurs from July to March, peaking in November to March (the austral summer). He reached no conclusions about seasonality of spawning in *C. melampygus*, but he documented ripe gonads throughout the austral spring and summer (September to March).

Based on visual underwater observations of spawning behavior between Cebu and Bohol in the Philippines (10°N lat.), von Westernhagen (1974) concluded that the main spawning season of *C. ignobilis* was December and January, with a lesser peak in June. "Limited but noticeable" behavioral spawning activity was reported throughout the year for a group of carangid species that included *C. ignobilis*, but it is not clear in what months *C. ignobilis* specifically was observed spawning. This seasonal trend based on observed behavior at low northern latitudes differs from the trend indicated at higher latitudes by our examination of gonads. Von Westernhagen also found that gonads of dissected specimens were always only partly ripe, suggesting serial spawning over a prolonged seasonal period.

In our study, female *C. melampygus* became sexually mature at about 350 mm SL, which is about 39% of L_∞. The calculated age of a 350 mm *C. melampygus* is close to 2 years. Female *C. ignobilis* mature at about 600 mm SL, about 33% of L_∞, at an estimated age of about 3½ years.

Williams (1965) estimated that the onset of sexual maturity in *C. melampygus* in east Africa occurred at about 30–40 cm (apparently SL). The basis of this estimate is not clear, but it agrees well with our results for the NWHI. In southern Africa, van der Elst (1981) indicated that maturity in this species occurred at 40 cm FL (source of information not stated). From plots of standard length and weight frequency of more than 330 *C. ignobilis*, Williams (1965) surmised that maturity was reached between 54 and 61 cm (apparently SL), and between about 3 and 5 kg. Both this length and weight estimate are consistent with our results. Van der Elst (1981) stated that "sexual maturity coincides with a fork length of 60 cm and an age of approximately 3 years."

Fecundity in our study was estimated only for *C. melampygus*. The equation relating fecundity to weight suggests a strongly nonlinear increase in fecundity with increasing body weight. *Caranx melampygus* appears to be a highly fecund species with a profligate reproductive pattern common to many pelagic marine fishes.

Diet

The diet of *C. ignobilis* contained a considerable diversity of fish types and invertebrates (Table 3). The perciform and tetraodontiform fishes were very important, but eels, crustaceans, and cephalopods were also significant in numbers and volume. The large number of reef fishes suggests that *C. ignobilis* spends much of its time foraging over shallow-water reef habitats, but the presence of squid and the schooling carangid *Decapterus macarellus* indicates exploitation of more open-water habitats as well. Diet results of Williams (1965) from east Africa also indicate feeding at all levels in the water column and probably over a variety of substrates. The presence in the diet of nocturnally active species such as eels, lobsters, and octopus suggests at least partly nocturnal feeding habits. Okamoto and Kawamoto (1980) concluded that *C. ignobilis* "appeared to be primarily a night feeder" in the NWHI. Van der Elst (1981) characterized this species in southern Africa as "more active during the day, especially at dusk and dawn."

C. melampygus appears to be more dependent on diurnally active, shallow-water reef fishes (Table 4). The labrids, mullids, pomacentrids, scarids, and monacanthids, which made up over 80% of its diet (percent

of summed IRI), are among the more common reef fishes in the NWHI (Parrish et al. 1985). No deep-water or pelagic species were represented in the diet, which suggests that *C. melampygus* associates closely with shallow-water reefs. The relatively low incidence of nocturnally active prey items suggests that this species is primarily a diurnal or crepuscular feeder. Based on their studies in the NWHI, Okamoto and Kawamoto (1980) also believed that it feeds mostly diurnally. On Hawaii Island, Hobson (1974) concluded that it probably feeds most often during early morning and late afternoon. In southern Africa, van der Elst (1981) stated that "while most active during early morning and late afternoon, it also hunts at night."

Little information is available on the diets of these two *Caranx* species in Hawaii or elsewhere. Okamoto and Kawamoto (1980) made the following brief, summary report, based on examination of the guts of 104 *C. ignobilis* and 27 *C. melampygus* from the NWHI: "Stomach contents of (*C. ignobilis*)...included spiny and slipper lobsters, shrimps, portunid crabs, octopuses (*Octopus cyanea* and *Octopus ornatus*), eels, cornetfish, squirrelfishes (family Holocentridae), and surgeonfishes. The omilu (*C. melampygus*) on the other hand, was primarily a diurnal fish feeder with piha (*Spratelloides delicatulus*) comprising the bulk of its diet." Small, incidental collections of *C. melampygus* guts at South Kona (Hobson 1974, five specimens with prey) and South Kohala (Parrish, unpubl. data, three specimens with prey) on the west coast of Hawaii Island contained fishes, shrimp, stomatopods, and mysids.

Only fishes (including the serranid *Anthias* and a carangid) were found in the guts of four *C. melampygus* examined by Randall (1955) from the Gilbert Islands and two specimens examined by Hiatt and Strasburg (1960) from the Marshall Islands. Randall (1980) also reported on fish prey in the guts of 44 specimens of *C. melampygus* from the Marshall Islands, Hawaiian Islands, Line Islands, Marcus Island, Solomon Islands, and the Red Sea. Prey groups included eels, Caracanthidae, Serranidae (*Anthias* spp.), Priacanthidae, Carangidae, Caesionidae, Mullidae, Pomacentridae, Cirrhitidae, Labridae, Gobiidae, Acanthuridae, and squid. He also found food in the guts of seven specimens of *C. ignobilis* from the Marshall Islands, Line Islands, Hawaiian Islands, Pitcairn Group, and the Marquesas (Randall 1980). Prey included Scorpaenidae, Scaridae, and Acanthuridae.

Off east Africa, Williams (1956, 1965) reported only the percent of *C. ignobilis* specimens that contained each prey category (frequency percent) from 170 specimens that contained identifiable prey. His results included eels (0–2%), Synodontidae (0–1%), Plotosidae (0–1%), Belonidae (*Tylosurus* sp.) (1–2%), *Atherina* sp. (1–2%), Carangidae (0–2.5%), Leiognathidae (0–1%), Sphyraenidae (0–1%), Scaridae (2.5–6%), *Siganus* sp. (1–2%), Monacanthidae (0–1%), Tetraodontidae (0–1%), shrimp (0–2%), stomatopods (including *Squilla* sp.) (6–10%), and cephalopods (including squid) (2.5–4%). Including many unidentified prey groups, 79–84% of *C. ignobilis* contained fish, and at least 12% contained crustaceans. Similar analysis of 89 *C. melampygus* specimens containing prey (Williams 1956, 1965) indicated the following frequency percent for prey categories: Holocentridae (0–3%), Scorpaenidae (0–2%), *Caesio* spp. (2–13%), Lutjanidae (including *Lutjanus* sp.) (2–3%), Mullidae (0–2%), Labridae (0–2%), Scaridae (5–7%), and stomatopods (0–2%). Altogether, 97–100% of these specimens contained fish (many unidentified).

Based on all available results, the diets of both *Caranx* species appear to be strongly dominated by fishes; *C. melampygus* was considerably more limited to fishes in our study. Both jacks ate a wide variety of species and ecological types of fishes. In both, the labrids, scarids, mullids, and priacanthids were among the most important prey, and pomacentrids and monacanthids were at least moderately abundant. All these families except monacanthids were reported in the earlier studies of the diet of *C. melampygus*.

Scarids occurred more widely and abundantly in the diets than any other fish family. This result may be biased by the ease of identifying scarid dental plates among digested fish remains. No scarids could be identified to lower taxa. Scarids may be somewhat more important to *C. ignobilis*. Labrids were important by all measures in our study (especially for *C. melampygus*) but less prominent in the reports of others. Eels were rather widely reported in the diets of both species. At least two eel families were represented in each species in our studies (a total of three eel families). Their considerable abundance in *C. ignobilis* suggests frequent, active feeding close around reef structures or other substrates that provide good cover. Seven *C. ignobilis* individuals in our study contained more than one eel each; one contained both a muraenid and a congrid eel.

Monacanthids probably are taken commonly by these jacks when monacanthid densities are normal. However, the heavy consumption indicated by our data is probably a result of an unusual population explosion of the filefish *Pervagor spilosoma* that occurred during the course of the study. The monacanthids in *C. ignobilis* were not further identifiable, but 24 of 28 monacanthid individuals in *C. melampygus* were identified as *P. spilosoma* and the other four as the genus *Pervagor*. Fourteen of the 15 incidents of predation (involving 27 of 28 prey individuals) occurred between late June 1982 and late March 1983 (when field work ended). These incidents began with the first sizable collections of jacks after the surge in the filefish

population was initially observed in visual censuses. Census counts of *P. spilosoma* remained high to the end of the study. This temporal pattern of predation and prey abundance appears to offer an example of opportunistic feeding on sporadically abundant prey. The much higher incidence of *P. spilosoma* in *C. melampygus* appears to reflect the specific locations and timing of sampling relative to the filefish population surge.

Potts (1980) analyzed the predatory behavior of *C. melampygus* at Aldabra Atoll (Indian Ocean). His observations indicated that this species sometimes forages in small groups, but that it is most often found singly or in pairs. Major (1978), who conducted an investigation of the predator-prey interactions of a captive group of juvenile *C. ignobilis* in Kaneohe Bay, Hawaii, showed that there are advantages to group hunting of schooling fish. *Caranx* species are known to form interspecific feeding associations with large labrids and other predatory species such as sharks, barracuda, sting rays, and eagle rays (Potts 1980). *C. melampygus* sometimes follow species that disturb the substrate, causing small fishes and crustaceans to be flushed out and exposed (Hobson 1974; pers. observ.). Some of the small crustaceans and gastropods found in the guts of *C. melampygus* may have been taken in this way.

Potts described *C. melampygus* as a diurnally active predator that increased hunting activity at dawn and dusk, when small midwater planktivorous fishes are moving to or from the shelter of the reef. These observations are generally consistent with our analysis of the feeding habits of this species in Hawaii. However, nocturnal fishes and crustaceans occurred in some of our samples, and planktivorous fishes did not dominate the diet.

The total incidence of benthic invertebrate prey in our specimens was considerable: 43% (frequency) for *C. ignobilis* and 22% for *C. melampygus* (including all cephalopods). *Caranx ignobilis* is one of the few fishes known to consume large, fully adult lobsters (Gooding 1985). Lobsters occurred in about 4% of the specimens, composing over 10% of the diet by volume in our study (Table 3). Okamoto and Kawamoto (1980) also reported this interaction, and Gooding (1985) observed such predation in the field. Lobsters are large, long-lived invertebrates that appear to be situated high in the benthic trophic system. This is one of several links that suggests that these large, abundant *Caranx* species, with their high rates of food consumption, are particularly important apex predators (Table 6).

Large crustaceans occur rather widely in the diets reported for *C. ignobilis* and *C. melampygus* (Williams 1956 and 1965, Hobson 1974, Okamoto and Kawamoto 1980, Parrish unpubl. data). In our study, the frequency of occurrence and numerical percent of crustaceans in the diet were sizable, but the low volumes for groups other than lobsters suggest that their dietary role is quantitatively minor (Tables 3 and 4). Many crustaceans could not be identified to low taxonomic level, but the major groups found in these *Caranx* species appear to be among those most common in the diets of a wide range of other carnivorous, demersal fish species in the NWHI, e.g., shrimp, crabs, and stomatopods (Parrish et al. 1985). All these major groups have also been reported in other diet studies of these jacks.

The higher incidence of crustaceans in smaller individuals of *C. melampygus* in our study was not obviously related to characteristics of the habitat or social structure. Fish of many sizes (larger and smaller than 350 mm SL) overlapped broadly among habitats, both in our collections of specimens and in many field observations. Benthic sampling in the NWHI suggested that large crustaceans were widely available in most of these types of habitats. No direct evidence is available to confirm the basis of this size difference in diet of *C. melampygus*; it may reflect changing food preference with age and the ability of larger individuals to capture larger fish as prey. (All the crustaceans found in *C. melampygus* specimens of all sizes could probably have been captured easily by even the smallest of the specimens.)

In our study, *C. ignobilis* consumed both the benthic/demersal octopus and the more pelagic squid in quantities (Table 3) that suggest that this trophic interaction is ecologically important to predator and prey populations. Only two specimens of *C. melampygus* contained cephalopods. There have been occasional previous reports of cephalopods in these jack species (Williams 1956, Okamoto and Kawamoto 1980, Randall 1980).

There was a relatively low overlap of specific diet items between *C. ignobilis* and *C. melampygus* (index $A_{yz} = 0.42$), indicating some separation of feeding niches of these two sympatric congeners. Morphologically, they are very similar, but a mature *C. ignobilis* is considerably larger than a mature *C. melampygus*. This difference in body size probably accounts for the occurrence or higher incidence of larger prey individuals and some larger species (e.g., lobsters, octopus) in *C. ignobilis*.

Energy budget and population consumption

Preliminary energy budget calculations and estimates of food consumption were made for jack populations primarily for their ecological interest. Clearly, the estimates of energy budget terms are crude and may be of limited value from a physiological perspective.

Measured ration of fish feeding *ad libitum* while swimming actively in a relatively undisturbed captive environment was used as an estimate of the natural, long-term, average ration of fish in the wild. If feeding were not reduced by trauma or behavioral effects of captivity, such feeding should provide an estimate of maximum natural ration, given superabundant, easily accessible food. Since the measured growth rate in captivity closely approximated the growth rate estimated for wild fish by the von Bertalanffy model, it may be that the effects of captivity depressed the *ad libitum* feeding activity from the maximum rate, to approach the natural, long-term, average rate. In any case, there is no clear direction of bias and no obvious way to improve the estimate of natural ration.

For the parameters k and γ, there seem to be no data specifically for these jacks or for closely related species. Published values for a considerable number of rather large, active, perciform fishes are similar to those chosen in this study (about 0.8 for both parameters) (e.g., Winberg 1956). The value of k chosen affects the entire calculation of captive α and subsequently of C for all weight-classes. The value of γ affects the entire calculation of captive α, but affects only one term (the largest) in the subsequent calculation of C. For each of these parameters, because it occurs in the calculation of captive α and subsequently of C, the effects of any inaccuracy in the choice of the value tend to cancel.

Use of a single value of α for all sizes of fish introduces another assumption. In previous work, this coefficient has often been treated as constant over a considerable range of sizes (Winberg 1956). However, for most species, α has not been determined for large sample sizes or large size ranges. A rather extreme range of sizes is included in the present calculations. No adequate measurements were available to produce a direct estimate of α for *C. ignobilis*. The use in its place of the α calculated for *C. melampygus* represents an approximation, and thus the estimated components of the energy budget for *C. ignobilis* may be less reliable. However, the similarity of α values presented by Winberg (1956) for a wide variety of less closely related species suggests that the approximation used is acceptable. Temperatures in the seawater feeding tanks were close to normal sea temperatures throughout the year, and therefore no correction of α for temperature seemed necessary. (The full annual range of tank and sea temperatures was small.)

The quality of the estimate of growth rate depends upon the quality of the fitted von Bertalanffy model as a descriptor of actual growth. Both regressions were good fits, and t_0 and L_∞ values were realistic. The use of dW/dt, evaluated for each chosen weight-class, is probably the best estimate of growth rate available from the von Bertalanffy model.

The estimate of reproductive output is crude, but little else is available. Since whole body weights were used in the von Bertalanffy model regressions, at least part of the reproductive energy may be viewed as included in the growth rate term, G (on some sort of average basis across all specimens and seasons). However, since the development of reproductive products is seasonal, it seemed reasonable to add a term representing the weight of a fully developed gonad to represent additional annual reproductive energy demand. The effects from both these terms may somewhat overestimate reproductive demand. However, multiple clutches may be developed over the course of a year, so the gonad weight alone may underestimate the actual reproductive energy.

As in all such energy budgets for active animals beyond the early juvenile stages, the respiratory metabolism term, Q, was dominant (see Table 5). The growth term, G, was never more than 10% of Q for the size-classes calculated here, and the reproductive term, S, was always substantially less than G. Therefore, factors affecting the accuracy of the components of Q (e.g., assumptions about the parameters α and γ) produce the greatest effects on the total estimate of the ration, C.

Components of the basic energy budget derived in this study, e.g., growth parameters (L_∞, W_∞, K, and t_0), maximum GSI, and α, should be similar in other tropical and subtropical localities where these species occur. The value of α (and corresponding metabolism and ration) can be readily adjusted for other temperatures by using Krogh's (1959) "normal curve" or corresponding mathematical functions (e.g., Winberg 1956:32, Ursin 1967:2396).

The estimate of population consumption in the specific case of FFS was of particular interest because of the extensive community trophic work done there. A mathematical trophic model of the shallow marine ecosystem there has been produced (Polovina 1984), with the biota lumped into a dozen large trophic compartments. Jacks (especially these two *Caranx* species) are major members of one of the top trophic-level compartments. Comparison of our numbers for consumption with those from the model suggests that these jacks provide an even more important trophic path than the large-scale model predicts.

The census methodology used to produce the population estimates in Table 6 was not designed to adequately census such wide-ranging, highly mobile species, and these estimates must be considered rough. They probably represent maximum estimates. No method was found to check them directly. Extrapolation of the catch data for the year 1900 from the main Hawaiian islands produced an estimated "catch" for FFS of about 44 *C. melampygus*/km^2 and 26 *C. ignobilis*/km^2.

This is an order of magnitude lower than the visual census estimates of full populations of 460/km^2 and 260/km^2, respectively. There is no basis for estimating accurately what fraction of the standing stock of either species was caught in 1900. However, there is no evidence that the fishery was immediately depleted, so it seems likely that the standing stock was several times the annual catch for each species. It seems reasonable that the actual present stock sizes at FFS are not much greater than the figures in Table 6, and they are probably not less than a third of those estimated figures.

Based on our study, it is clear that populations of these two species combined eat at least a few thousand metric tons annually at this medium size atoll (about 500 km^2 in area to a depth of about 20 m). From an ecological perspective, this must represent one of the most important top-level trophic paths in this system (and probably in many others). The estimated combined predation pressure (Table 6) by these two jacks exceeds the combined estimate for the three dominant shark species in the same system (DeCrosta et al. 1984) by a factor of about 40. This source of mortality should be considered in any quantitative examination of the population ecology of the prey groups, particularly fish, large crustaceans, and cephalopods. The diet composition results in Tables 3 and 4 permit such analysis at lower systematic levels as well.

The information now available about these two important jacks provides an outline of their life history and trophic ecology. Both species are moderately fast growing, attain large size, and live at least several years. Both mature at relatively large size (a major consideration in fishery management), have apparent high fecundity, and may reproduce for at least 4–6 years, with a pronounced seasonal spawning cycle. These jacks are highly piscivorous, but show considerable quantitative separation in their specific diets. *Caranx melampygus* is more dependent on fishes, whereas *C. ignobilis* has a more varied diet that includes large crustaceans and cephalopods. Both species have high metabolic demands and correspondingly high rates of food consumption. Large populations of these species may impose considerable predation mortality on benthic/demersal communities, particularly on fishes. These jacks are potentially of interest in many shallow-water tropical environments because of their role in community ecology as well as in local fisheries.

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Appendix A

Numbers of increments visible by scanning electron microscopy in the otoliths of various size specimens of *Caranx melampygus* and *Caranx ignobilis*, and corresponding estimated ages of specimens (assuming daily deposition of increments).

Caranx melampygus			*Caranx ignobilis*		
Length of fish (mm SL)	No. of otolith increments	Estimated age (yr)	Length of fish (mm SL)	No. of otolith increments	Estimated age (yr)
122	186	0.510	106	274	0.751
196	486	1.332	109	276	0.756
210	458	1.255	113	293	0.803
259	598	1.638	462	793	2.173
270	612	1.677	485	846	2.318
283	596	1.633	606	1580	4.329
294	423	1.159	660	1690	4.630
320	687	1.882	760	1793	4.912
328	812	2.225	985	2387	6.540
341	710	1.945	1180	3384	9.271
380	813	2.227			
468	904	2.477			
555	1435	3.932			
660	2154	5.901			

Appendix B

Estimated batch fecundity for 11 gravid female specimens of *Caranx melampygus* of various sizes.

Length of fish (mm SL)	Whole wet weight of fish (g)	Whole wet weight of ovary (g)	Est. no. of eggs in ovary
328	760	14.1	49,700
465	1985	46	284,000
502	2590	78.5	774,000
503	2724	133	987,000
514	3667	182	888,000
520	3807	224	2,600,000
596	5167	292	1,690,000
617	5650	210	1,020,000
640	6490	440	4,270,000
649	6615	223	1,540,000
654	6220	249	2,220,000

Observations on the Paralarval Ecology of a Euryhaline Squid *Lolliguncula brevis* (Cephalopoda: Loliginidae)

Michael Vecchione

Systematics Laboratory, National Marine Fisheries Service, NOAA
National Museum of Natural History, Washington, D.C. 20560

Abstract. – Cephalopods were examined from more than 3000 zooplankton samples collected over a two-year period from coastal and estuarine waters of southwest Louisiana. In total, 270 cephalopods were taken in 164 of these samples; 267 specimens from 161 samples were *Lolliguncula brevis*. They were found in coastal waters from April through January, but in estuarine waters only in May, July, and August. Maximum standardized abundance was found in the nearbottom waters of the estuary in May. Overall, paralarval *L. brevis* were most often collected nearbottom in inshore coastal waters during May–June. This species was not collected in the estuary at salinities below 27×10^{-3}. Although they were found in coastal waters with lower salinities (22×10^{-3}), abundance was generally greatest in waters with salinities of about 26×10^{-3}. Somewhat surprisingly, paralarval *L. brevis* were collected throughout the range of dissolved oxygen concentrations sampled, including waters considered to be hypoxic, with <2 mL/L dissolved oxygen. Contents of the digestive tract were examined in 50 paralarvae; 18% of these contained solid food while others were inflated with a semiliquid mush or clear liquid.

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The squid genus *Lolliguncula* is interesting from an evolutionary viewpoint because this coastal genus includes the only species of cephalopod known typically to inhabit low-salinity estuaries, *L. brevis*. Thus, it is a clear-cut example of adaptive radiation of the stenohaline Class Cephalopoda toward euryhalinity. Adaptation to an unusual environment may involve physiological or behavioral changes in an organism at any point in its life history. The physiology of euryhalinity in this species has been studied using trawl-caught squids from Galveston Bay, Texas (Hendrix et al. 1981, Segawa and Hanlon 1988, Wells et al. 1988). The distribution of adults and advanced juveniles has been reported from trawling studies of estuarine and coastal waters of Texas (Hixon 1980) and Florida (Dragovich and Kelly 1963 and 1967, Laughlin and Livingston 1982). Although morphological aspects of the development of this species have been described (Hall 1970, Hunter and Simon 1975, McConnathy et al. 1980, Vecchione 1982b), the only published report on the distribution of paralarvae (see Young and Harman 1988 for a discussion of the term) was a brief note on distribution near the northern limit of the species' range (Vecchione 1982a).

Studies of the early life history of cephalopods have been relatively infrequent because of logistical and taxonomic difficulties (Vecchione 1987). However, such studies should eventually be useful for comparisons with other taxa in the development of early-life-history theory (Vecchione 1986). I report here on the distribution of paralarval L. brevis collected during two concurrent studies of zooplankton and associated hydrographic parameters in the coastal and estuarine waters of southwest Louisiana.

Vecchione (1987) concluded that starvation resulting from failure of first feeding may contribute substantially to cephalopod mortality and subsequent recruitment failure. Therefore, the contents of the digestive tracts in a subset of the specimens also were examined to determine whether paralarval feeding by *L. brevis* is amenable to study.

Materials and methods

Details of the collection methods have been presented by Vecchione et al. (1983). The collecting methods differed as described below, reflecting the two separate studies that were conducted concurrently over a two-year period.

The coastal study used a 60 cm opening/closing bongo sampler for triplicate one-minute tows at two discrete depths (three depths during February–April 1981) at nine stations monthly for 22 months, February 1981–November 1982 (Fig. 1, M and D stations). Towing speed was 1.5–2.5 knots. Most stations were located at the 10 m isobath and the

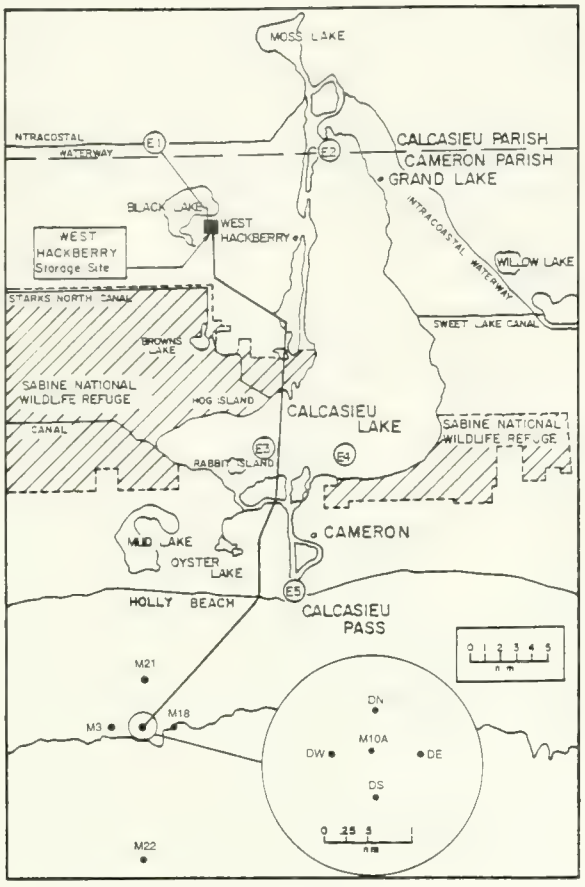

Figure 1

Locations of stations in southwest Louisiana. Estuarine stations are labeled E and coastal stations are labeled M and D. Station M18 was located on the 10 m isobath and station E5 was located at the coastline in Calcasieu Pass. Freshwater was diverted from the intracoastal waterway at station E1 and pumped to West Hackberry for solution-mining of a salt dome for a Strategic Petroleum Reserve storage site. A pipeline then transported the supersaturated brine to a diffuser at station M10A for discharge.

depths sampled were nearsurface (1–2 m depth) and nearbottom (~5–9 m depth). At the shallow station, M21 (5 m depth), and the deep station, M22 (14 m), the nearsurface tows were as described above but the nearbottom tows were modified to reflect local water depth. The bongo frame was rigged with 505 μm and 333 μm mesh nets, and both sides had flow meters mounted off-center inside the mouth to estimate the amount of water filtered for each sample. Most sampling was conducted during daytime because of contractual requirements. One station (M18) was resampled at night on the same day as regular monthly sampling for 9 months (June 1981, April–November 1982), to allow diel comparisons to be made; station DW was also resampled at night for the final two months. Before sampling at each station, temperature, conductivity, dissolved oxygen, and pH were measured *in situ* with a Hydrolab 6000 probe at one-meter intervals from bottom to surface.

During the same time period, the nearby Calcasieu Estuary was sampled at 5–6 stations (labelled E1–E5 on Fig. 1) monthly for 21 months, February 1981–October 1982. This estuary is very shallow (average high-tide depth <2 m), except in dredged channels, and sampling methods were constrained by the shallow stations (Stubblefield and Vecchione 1985). Triplicate one-minute samples were collected with two samplers described and figured by Stubblefield et al. (1984). The primary gear used at all stations was a half-meter ring net with 153 μm mesh mounted in a frame designed to eliminate avoidance due to bridle or boat wake. At three stations (E2, E3, and E4), an epibenthic pullsled rigged with 153 μm mesh netting was also used for 12 months, May 1981–April 1982, to examine vertical distribution in this very shallow water column. Flow meters were used with both samplers to estimate the amount of water filtered for each sample. At each station, physical parameters were measured similarly to the coastal stations. Sampling was timed to coincide with daytime high tide.

All samples were sorted for cephalopods. These were identified and individually measured (dorsal mantle length, DML). Standardized abundance in each sample was calculated as the number of *L. brevis* collected per 100 m^3 of water filtered. The 12 samples collected at each coastal station filtered a total of about 150–250 m^3 of seawater.

The questions that I wanted to address with these data can be grouped into two categories: (1) Description of large-scale patterns such as seasonal occurrence and overall distribution of the paralarvae with regard to temperature and salinity, and (2) statistical inference of small-scale patterns of abundance within waters in which the species occurs. Therefore, the data were treated differently depending on the category to be addressed.

In the first category, the description of paralarval distribution with respect to physical data (e.g., Fig. 3, the temperature-salinity diagram showing occurrence of *L. brevis*) is based on physical data at the sampled depths of all stations, including negative stations (where no paralarvae were taken), to contrast conditions under which they were collected from those where they were not, for all months in which *L. brevis* was collected at any station. Because the presence of paralarvae is limited in time to a brief period after seasonal hatching, including physical data for months in which they are not hatching would provide no infor-

mation on the abiotic dimensions of the paralarval niche.

For the second category, I wanted to determine average abundance within the water masses in which paralarval *L. brevis* were found, rather than average abundance throughout the entire geographic area. Because the paralarvae are planktonic and presumably stay within the water masses into which they hatch, average abundance would be artificially depressed if stations from other water masses (i.e., outside of the small-scale paralarval range) were included in calculations. For instance, physical conditions were sometimes very different at one or more stations because a coastal front divided the stations, so that *L. brevis* was collected in one group of stations but not in the other. Under those circumstances, including the water filtered at stations where the species was absent in the calculation of the number of *L. brevis* per m^3 of coastal water that month would not be an accurate representation of small-scale abundance. Descriptive statistics presented below are therefore based only on stations that collected *L. brevis*. For example, mean abundance for a month is the average of all samples, including negative ones, at all stations from which *L. brevis* were collected, but does not include negative stations. The statistical tests of hypotheses presented below were likewise based on the assumption that, if all twelve samples at a station failed to collect *L. brevis*, that station was extralimital for the paralarvae. For all tests of hypotheses, statistical significance was defined *a priori* as $\alpha = 0.05$.

Fifty digestive tracts were examined. Specimens were selected arbitrarily to be representative of the paralarval size range. Specimens were cleared with trypsin and then transferred to glycerol, allowing direct examination of the intact esophagus, stomach, caecum, and intestine for food remains (Vecchione In press a).

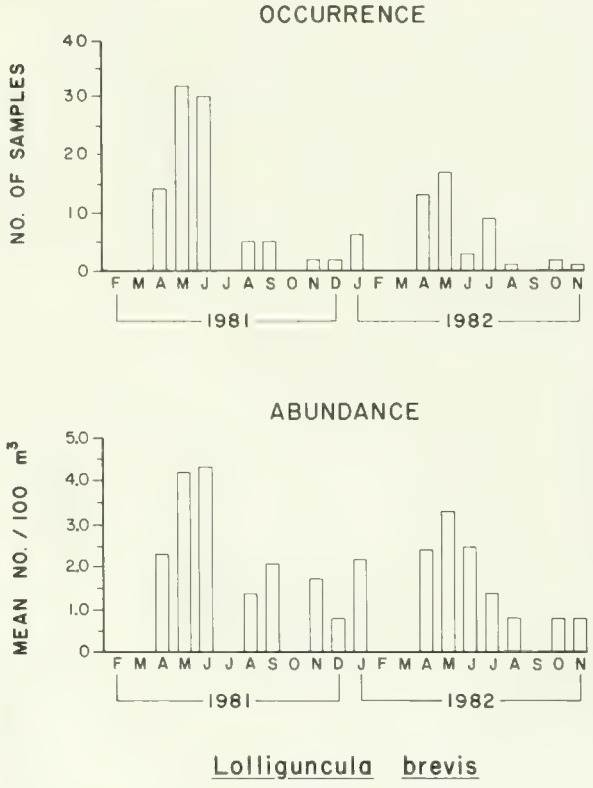

Figure 2

Seasonal distribution of paralarval *Lolliguncula brevis* in coastal Louisiana waters. (Top) Number of positive samples (out of 108 samples/month); (bottom) mean number of paralarval *Lolliguncula brevis* collected per 100 m^3 of water filtered at positive stations. The 108 samples collected per month filtered ~2000 m^3.

Results

In all, 3159 zooplankton samples were collected. Two hundred seventy cephalopod paralarvae were collected in 164 samples. These included two *Loligo* sp., one *Illex* sp., and 267 *Lolliguncula brevis*. The *L. brevis* came from 161 samples and ranged in length from 1.1 to 13.6mm DML.

Coastal distribution

Mesh comparisons Paralarval *L. brevis* were collected with 505 μm mesh in 75 samples and with 333 μm mesh in 77 samples. The Wilcoxon paired-sample, signed-rank test was used to compare both abundance and size of paralarval *L. brevis* in the two mesh sizes of the bongo samples. Neither abundance nor size of the paralarvae differed significantly between mesh sizes. Therefore, in the following analyses the bongo samples are considered as a single data set regardless of mesh size.

Seasonal patterns Paralarval *L. brevis* were collected from April through January (Fig. 2). Both the highest average abundance (mean $N/100\,m^3$) and the highest frequency of occurrence (number of samples that collected *L. brevis*) were found to occur in the spring (April–June) of both years. There appeared to be a slight tendency toward a bimodal seasonal distribution with a late-summer abundance minimum, similar to what I have found in many species of ichthyoplankton collected in these samples (unpubl. data).

Hydrographic relationships During the months in which *L. brevis* were collected, they were found

throughout the sampled temperature range, but were not collected at salinities of $<22 \times 10^{-3}$ (Fig. 3). Maximum abundance and frequency of occurrence were both associated with salinities of about 26×10^{-3}. Somewhat surprisingly, paralarval *L. brevis* were collected throughout the range of dissolved oxygen concentrations sampled, including waters considered to be hypoxic, with <2mL/L dissolved oxygen (Fig. 4).

Diel variability Mean abundance and mean DML were compared between the night and day samples at the same stations on the same day. Abundance was somewhat greater during daytime (day 2.9/100m^3; night 1.7/100m^3), specimens caught at night tended to be somewhat larger (mean DML: day 2.0mm; night 2.3mm), but neither of these differences was statistically significant at the *a priori* α-level (t-test: abundance P 0.276, size [DML] P 0.600).

Vertical distribution Paralarvae were much more abundant nearbottom (mean abundance 4.7/100m^3) than nearsurface (0.7/100m^3). Statistically, this trend was very significant (t-test, $P<0.0001$). The paralarvae collected nearbottom were significantly larger (mean DML 2.1mm) than those collected nearsurface (1.6mm, t-test, P 0.049).

Variability among stations Abundance tended to be greater inshore at station M21 than farther offshore (Table 1) but, based on analysis of variance (ANOVA), this difference was not statistically significant (P 0.264). Similarly, paralarvae collected inshore tended to be larger than those offshore (Table 1), but this tendency also was not statistically significant (ANOVA, P 0.610). There was no obvious pattern of occurrence (number of samples) among stations, nor obvious patterns of changes in abundance or size alongshore.

Estuarine distribution

Whereas 237 *L. brevis* were collected in 152 coastal samples (5% of samples),

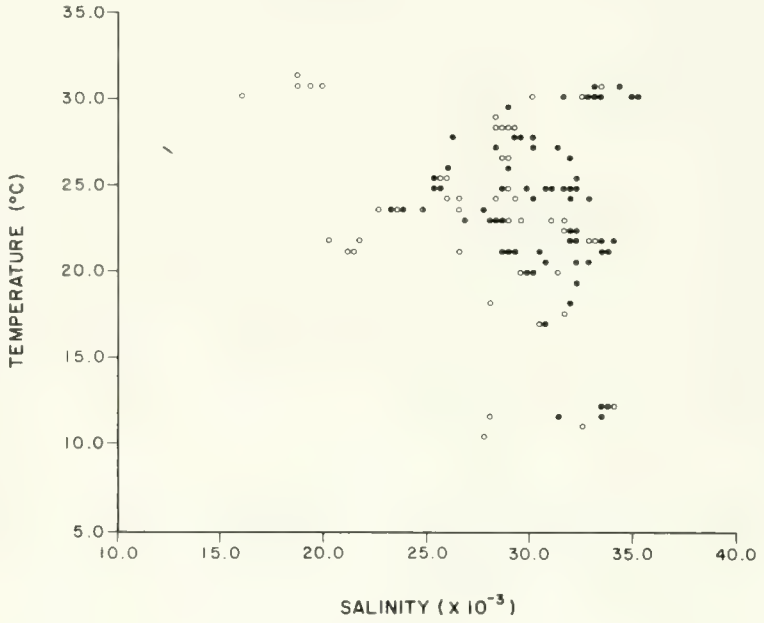

Figure 3
Occurrence of paralarval *Lolliguncula brevis* with respect to temperature and salinity. (Solid circles) Samples that collected *Lolliguncula brevis*; (open circles) samples that did not. Each circle may represent more than one sample.

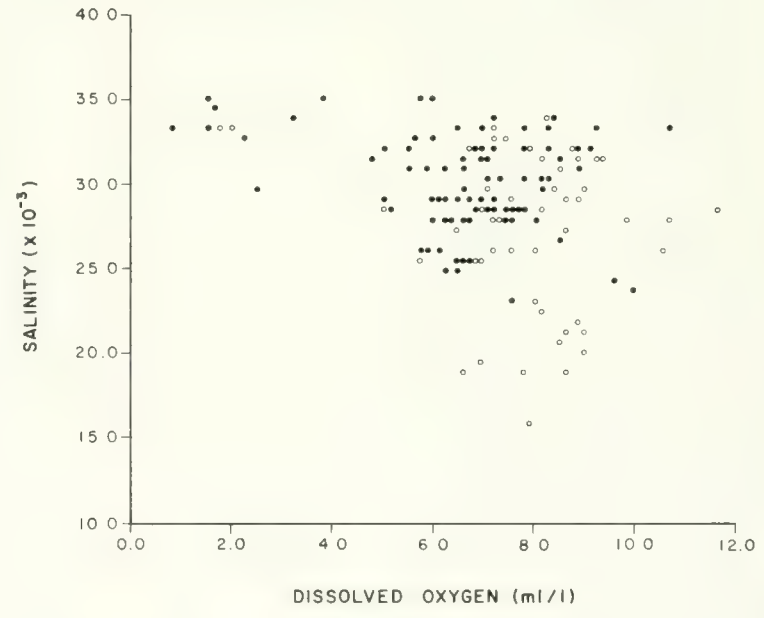

Figure 4
Occurrence of paralarvae with respect to salinity and dissolved oxygen. (Solid circles) Samples that collected *Lolliguncula brevis*; (open circles) samples that did not. Each circle may represent more than one sample.

Table 1
Distribution of paralarval *Lolliguncula brevis* at stations where paralarvae were present.

Station	Abundance (N/100 m^3) Mean	SD	Size (mm DML) Mean	SD	Occurrence (N of samples)
Coastal					
M21	5.7	25.8	2.4	3.0	15
M18	2.8	5.9	2.0	0.9	29
DE	2.5	4.7	1.7	0.4	14
DN	3.3	6.3	2.8	2.2	10
M10A	1.5	3.6	2.2	1.3	12
DS	2.8	6.8	1.8	0.3	14
DW	1.7	3.8	2.4	1.4	12
M3	4.0	17.5	2.0	0.4	27
M22	2.1	4.3	1.7	0.3	19
Estuarine					
E5	4.4	5.3	2.1	1.1	4
E4	5.0	8.3	2.0	0.2	2 (1 pullsled)
E3	78.3	105.9	3.4	4.1	3 (all pullsled)
E2	0	—	—	—	0
E1	0	—	—	—	0

only 30 were collected in 9 estuarine samples (2%; Table 1). The greatest abundance (270/100 m^3) calculated during this study from either estuarine or coastal waters came from an epibenthic pullsled sample taken at station E3 in May 1981; all pullsled samples from that location and time included large numbers of paralarvae (Table 1). Also, paralarvae from estuarine waters were significantly larger (mean DML 2.5 mm) than those from coastal waters (2.0 mm; t-test, $P<0.05$). Paralarvae were collected in the estuary only during May, July, and August. Although the estuarine sampling included waters that varied greatly in salinity, *L. brevis* were found there only in waters with salinities $>27 \times 10^{-3}$.

Paralarval feeding

Fifty paralarval digestive tracts were examined. Of these, 33 paralarvae were <2 mm DML, 12 were 2–3 mm DML, and 5 were >3 mm DML; the largest was 9.3 mm DML. The largest specimen had pieces of crustacean exoskeleton in the stomach and intestine but only fluid in the caecum. Of the other specimens >3 mm DML, one had nondescript solid chunks in its stomach, caecum, and intestine, one had fluid and ink in the stomach and caecum, and the digestive tracts of the other two were empty. In the 2–3 mm size-class, two contained solid chunks of unrecognizable food, four had liquid and semiliquid mush in their digestive tracts, and six were empty. Of the smallest size-class, one contained crustacean appendages, four had amorphous chunks of food (usually in the combined stomach/caecum, although one specimen had a chunk of food in the esophagus), fifteen had one or more of the digestive organs inflated with fluid, and thirteen were empty. Therefore, of the total sample 18% of the paralarvae had solid food material in the digestive system.

Discussion

Distribution

Paralarval *L. brevis* do not seem to be as euryhaline as the adults. Trawl-caught *L. brevis* are osmoconformers that are known to tolerate salinities as low as 17.5×10^{-3} (Hendrix et al. 1981) and have been reported from estuarine waters with much lower salinities ($<10 \times 10^{-3}$, Laughlin and Livingston 1982). Paralarvae, however, were not found at salinities $<22 \times 10^{-3}$, and were most abundant at higher salinities. This may in part explain why the paralarvae were rare in the estuary as well as why they were most abundant in nearbottom samples where the salinity is higher than near the surface in both coastal and estuarine waters of Louisiana (Vecchione et al. 1983). The estuarine paralarvae were larger, and presumably older, than those of coastal waters. Thus, although estuarine paralarvae were not found in low-salinity waters, it appears that the distribution of this species shifts toward the estuary with growth, perhaps because of the onshore set of the nearbottom currents. Euryhalinity may develop ontogenetically late during paralarval development.

The spawning location for this species in Louisiana waters is not known. Whereas *L. brevis* eggs have been reported in trawl studies from Tampa Bay, Florida (Hall 1970) and from bay and coastal waters off Texas (Hixon 1980), extensive trawling (Vecchione In press b) at the same coastal and estuarine stations as the zooplankton projects reported here failed to collect any squid eggs throughout the same time period as this study. In Galveston Harbor, Texas, *L. brevis* attaches its egg capsules to hard surfaces, sometimes covering crab traps so thickly as to make them useless for their designed purpose (A. Landry, Texas A&M Univ., Galveston, pers. commun., 1984). The Louisiana trawling study avoided areas of hard substrate and thus probably missed local spawning areas. Hixon (1980) reported that *L. brevis* egg capsules were collected off Galveston from March through December in depths of 2–18 m with salinities of $21–35 \times 10^{-3}$ and tempera-

tures of 16–31°C. Paralarval seasonality in Louisiana is similar to that of the eggs off Galveston; therefore, in the northern Gulf of Mexico, *L. brevis* appears to hatch year-round except for the coldest months. This contrasts with the situation around the mouth of Chesapeake Bay, near the northern limit of the species' range, where paralarvae are found only during the warmest months of late summer (Vecchione 1982a).

Laughlin and Livingston (1982) concluded that fluctuations in the abundance of trawl-caught *L. brevis* in the Apalachicola Estuary, Florida are related to zooplankton biomass in the estuary, and they implied that this relationship results from the squid feeding on planktonic copepods. Juvenile and adult *L. brevis* actually feed on larger prey, mostly nektonic fishes and shrimps (Hanlon et al. 1983). Therefore, I believe that the correlation that Laughlin and Livingston (1982) described results from covariance of squid and zooplankton abundance with other independent factors such as salinity and current patterns. However, planktonic copepods are likely the natural prey for paralarval *L. brevis*. Copepods in the zooplankton samples reported here were abundant year-round, with spring and fall abundance peaks; even during midwinter, abundances >1000/m^3 were common. Although the concentration of natural food required for successful feeding by the paralarvae is not known, it does not seem likely that food limitations are responsible for the seasonal distribution found for the paralarval squids. It is possible, though, that factors such as seasonal storms that affect transport processes or patch dimensions of the prey are as important as temperature in controlling paralarval seasonality.

Paralarval *L. brevis* were found most often near the bottom in nearshore coastal waters. However, an important layer of the water column that was not sampled is the surface microlayer. Paralarval *Loligo pealei* in the Middle Atlantic Bight were far more abundant in neuston samples than in samples from subsurface waters, although they were larger in subsurface waters (Vecchione 1981). I inferred from this pattern that *L. pealei* hatchlings ascend to the surface for first feeding on the concentrated zooplankton of the neuston, and then shift ontogenetically to deeper waters. Paralarval *L. brevis* were also larger in bottom waters than near the surface. Neuston samples in waters of coastal Virginia collected paralarval *L. brevis* in comparatively large numbers (Vecchione 1982a). Thus, this species may undergo a similar ontogenetic vertical migration, but nighttime neuston sampling would be required to test this hypothesis.

It was somewhat surprising that paralarval *L. brevis* were found in waters considered to be hypoxic. Recent evidence (Wells et al. 1988, Vecchione In press b) indicates, however, that this species is capable of adjusting to low concentrations of dissolved oxygen by increasing oxygen uptake rates. Although no experimental evidence exists to show when in the life history this capability develops, my distributional data suggest that the paralarvae also have some means of coping with hypoxia. This would be a very important adaptation for a bottom-spawning species in coastal waters of the northern Gulf of Mexico. The bottom waters of this area seasonally become hypoxic during the salinity-stratified conditions of midsummer (Pokryfki and Randall 1987, Turner et al. 1987), causing catastrophic changes in the benthic fauna (Harper et al. 1981, Gaston 1985) and shifts in the distribution of nekton (Pavela et al. 1983).

Feeding

This is the first published analysis of stomach contents for paralarval cephalopods. The incidence of solid food material in the digestive organs may appear to be low but, when compared with feeding studies on trawl-caught squids, does not seem unreasonable. For instance, Dragovich and Kelly (1963) found that among 1684 adult and juvenile *L. brevis* trawled from Tampa Bay, 80% of the stomachs were empty; of those <40 mm in "body length," 94% had empty stomachs. Similar results have been found for other species of loliginids. One substantial difference between the paralarval stomach contents and those of larger squids is the dearth of recognizable hard parts in the ingested food of the paralarvae. This makes identification of the prey organisms even more difficult for paralarvae than for adults and juveniles, which bite their food into pieces and then swallow the pieces whole, including skeletal material. However, paralarvae of another loliginid, *Loligo vulgaris*, when feeding on small shrimp, can remove and ingest the soft tissue of the shrimp and discard the exoskeleton (S. v. Boletzky, Laboratoire Arago, Banyuls-sur-Mer, France, pers. commun., 1985). Recently, immunoassay methods have been developed to allow specific identification of very small samples of macerated food (e.g., Theilacker et al. 1986); such methods may be required for identification of gut contents in paralarval squids.

Determination of the number of animals that had fed was further complicated by the lack of differentiation between the stomach and caecum in small paralarvae and the frequent presence of either clear fluid or mush-like fluid in the combined stomach/caecum. This fluid is reminiscent of the caecal fluid in older squids that are well along in digesting a meal. Alternatively, the fluid may be largely seawater swallowed either naturally or during fixation or may be spontaneously secreted digestive fluids. Without knowing the dynamics of

digestion in paralarvae, distinguishing among these alternatives is impossible. Paralarval feeding is a subject greatly in need of study (Vecchione 1987, Vecchione and Hand 1989), especially because starvation of paralarvae has been proposed as a dominant factor affecting the large interannual variability in recruitment of cephalopods.

Acknowledgments

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Interannual Variation in Growth Rates and Back-Calculated Birthdate Distributions of Pelagic Juvenile Rockfishes (*Sebastes* spp.) off the Central California Coast

David Woodbury
Stephen Ralston

Tiburon Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
3150 Paradise Drive, Tiburon, California 94920

Abstract.– Young-of-the-year pelagic juvenile rockfish (genus *Sebastes*) were collected during annual surveys in the spring and early summer, 1983–88, off the central California coast. Growth rates and back-calculated birthdate distributions of five species (shortbelly rockfish *S. jordani*, bocaccio *S. paucispinis*, chilipepper *S. goodei*, widow rockfish *S. entomelas*, and yellowtail rockfish *S. flavidus*) were estimated from daily otolith increments.

Interspecific variation in growth rates was evident, with bocaccio exhibiting the fastest growth (0.56–0.97 mm/day) and yellowtail rockfish growing slowest (0.19–0.46 mm/day). Growth rates of all species varied among years. Comparisons of annual growth performance, measured by predicting standard length at a selected standard age, revealed strong positive interannual covariation among the five species studied; in general, growth was relatively good in 1987 and was poor in 1985.

Back-calculated birthdate distributions also revealed strong positive interannual covariation among these species; most distributions were unimodal. The years 1985 and 1988 were characterized by distributions that were centered early in the year; whereas in 1986 (and possibly in 1983) these distributions occurred later.

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Fishery Bulletin, U.S. 89:523–533 (1991).

Understanding recruitment fluctuations and the interplay of factors affecting the establishment of year-class strength is the single most challenging issue in fisheries today (Rothschild 1986). In particular, rockfishes of the genus *Sebastes* are known to exhibit large fluctuations in recruitment (Leaman and Beamish 1984), wherein a single dominant year-class can sustain a fishery for a number of years. Rockfishes are an important component of the west coast groundfish fishery, with combined 1988 landings of 35,000 MT (PFMC 1989). Historically, rockfish stock assessments have relied almost exclusively on catch-at-age data (e.g., Hightower and Lenarz 1989); such analyses do not perform well in the absence of auxiliary information (e.g., an index of pre-recruit abundance). Knowledge of mechanisms affecting first-year survival could improve our ability to predict recruitment, which in turn could have major implications to the management of this group (Deriso et al. 1985, Methot 1989, but see Walters 1989).

In some situations starvation and food limitation have been shown to control larval abundance (Lasker 1981), although predation is believed to be important in others (reviewed in Sissenwine 1984, Bailey and Houde 1989). In either case, if mortality decreases with increasing size (Miller et al. 1988), larval and pelagic juvenile growth rates can have a major impact on survivorship during the first year of life. This is because fast-growing fish are exposed to high mortality rates for shorter periods of time (Houde 1987).

As part of an ongoing study to monitor annual fluctuations in the abundance of young-of-the-year pelagic juvenile rockfishes inhabiting the coastal waters off central California, the growth of five species (shortbelly rockfish *S. jordani*, bocaccio *S. paucispinis*, chilipepper *S. goodei*, widow rockfish *S. entomelas*, and yellowtail rockfish *S. flavidus*) was assessed through the study of otolith daily-increment microstructure formed during the pelagic larval and juvenile life stages (Jones 1986). Intraspecific differences in growth performance over the period 1983–88 were then examined statistically and trends were compared among species.

Birthdate frequency distributions of the fish that survived from birth to the time of sampling were back-calculated from aged subsamples, length measurements, and known dates of capture (Bolz and Lough 1983). These projected distributions were compared intraspecifically among years to evaluate whether the preponderance of juvenile survivors

came from larvae that were extruded early or late in the season. Birthdate distributions were also compared among species to reveal the extent of interspecific covariation in annual survivorship.

Methods

Midwater trawl collections

Annual 30-day cruises aboard NOAA's R/V *David Starr Jordan* began in 1983 and were conducted during late spring (May–June), a time when most pelagic-stage juvenile rockfishes are identifiable to species, but prior to their settling to nearshore and benthic habitats. The sampling gear used was a midwater trawl with a 26 m headrope and 169 m^2 net opening, equipped with a 0.945 cm (3/8″) inner liner. A standard haul consisted of a 15-min nighttime tow at a depth of 30 m covering a distance of roughly 1 km. Additional tows were made at other depths (i.e., 10 and 100 m) as time and bottom topography permitted.

From 1983 to 1985, the survey was designed to sample from nearshore waters out to a distance of 55 km (30 nmi) along transects located at 31 km intervals perpendicular to the coast. Sampling began at Pt. Sur (36°18′N) and continued northward until completion of the cruise. In 1986, the sampling design was modified to permit three "sweeps" through a study area bounded by Cypress Pt. (36°35′N) and Pt. Reyes (38°10′N) (Table 1). Four additional cruises were conducted in April of 1985–88. These cruises ranged from 5 to 10 days in length and were limited to the Gulf of the Farallones (1985–86), or covered one complete sweep of the study area (1987–88). Trawls were conducted at 5–7 stations per night along 7 transects during a sweep. Wyllie Echeverria et al. (1990) discuss the survey methodology in greater detail.

As many as 24 species of pelagic-stage juvenile rockfish were collected during a single cruise. All specimens were tentatively identified and frozen at sea. On rare occasions catches were subsampled when they were too large to enumerate. After 1987, length compositions of large trawl catches were based upon expansion from measured subsamples of each species.

Table 1
Summary of sampling dates for juvenile rockfish cruises. Asterisks indicate trawls limited to Gulf of the Farallones.

Year	Sweep	Dates	Stations
1983	1	8–24 June	18
1984	1	12–27 June	25
1985	1*	10–16 April	18
	2	31 May–30 June	37
1986	1*	13–22 April	30
	2	3–11 June	33
	3	11–18 June	28
	4	20–25 June	28
1987	1	10–20 April	34
	2	23 May–1 June	33
	3	2–12 June	34
	4	12–21 June	33
1988	1	16–22 April	28
	2	22–31 May	33
	3	2–9 June	33
	4	11–18 June	31

Otolith preparation and analysis

In the laboratory, species identifications were confirmed and fish were measured to the nearest 1.0 mm standard length (SL). For this study, the most important species were selected for age determination. A subsample of juveniles, measured to the nearest 0.1 mm, was selected for daily age analysis based on the size range encountered on each cruise. Specimens were selected at 0.5 mm intervals from the smallest to largest. The sagittal otoliths were removed, cleaned, and adhered concave (lateral)-side-down onto glass microslides using clear nail polish. To reveal the inner microstructure, otoliths were ground with wet 300–600 grit sandpaper and etched with HCl (Brothers et al. 1976).

A compound microscope with 40 and 100× objectives was used during otolith examination. Immersion oil was applied to the otolith, which was illuminated with polarized light. A closed circuit television camera was mounted on top of the microscope and the image was relayed to a video monitor. A digitizer with a precision of 0.13 μm was interfaced with the monitor and a microcomputer to accurately measure and record daily increments (e.g., McGowan et al. 1987). In combination, the equipment yielded an 800–2000× on-screen magnification range.

A computer program assisted in recording the distance from the nucleus to each increment, measured along the growth axis running from the focus to the postrostral margin. On occasion the periodic bipartite microstructure of daily increments was difficult to resolve within short (~50 μm) segments of the otolith. In these cases their number and width were interpolated by averaging the widths of the rings immediately preceding and following that segment, and dividing the mean into the segment length. Usually such averaging involved only about 10% of the total increments observed. In most cases (~80%), only one otolith was used unless it was damaged or destroyed

during preparation. Otoliths were read only once due to the destructive nature of the preparation method.

A photomicrograph of a shortbelly rockfish otolith (Fig. 1) shows increments that we interpreted to be produced daily. A dark ring followed by narrow, closely spaced rings was used as the starting point for enumeration of increments. The time of first increment formation is species-specific. Cases are known where fish larvae form the first increment at hatch, yolksac absorption, first feeding, or at other times (Jones 1986). Penney and Evans (1985), in their study of larval redfish (*Sebastes* spp.) off Newfoundland, noted a "heavy ring composed of a wide, translucent band followed by a prominent, high-contrast dark band" which they used as the first increment for age determination. Since all pre-extrusion larvae lacked the dark band and all planktonic larvae possessed it (some as young as 1 day), they assumed that it formed at the time of extrusion. Structurally, their extrusion check was quite similar to the marks seen in this study (Fig. 1). They, like us, also observed a number of thin, weakly expressed "pre-extrusion rings" laid down prior to the first increment (see also Campana et al. 1987). There are instances in which small (~4.8–5.0 mm) field-caught planktonic larvae of shortbelly rockfish lack the conspicuous first increment (T. Laidig, SWFC Tiburon Lab., pers. commun.). Faced with this uncertainty, we conclude that the first increment used in our counts forms some time between extrusion and first feeding. The distance of this first ring from the center of the focus varied among species (i.e., 12–17 μm), but was consistent within a species. The first few increments laid down after this early check ring typically were about 0.5 μm in width and they increased in size thereafter.

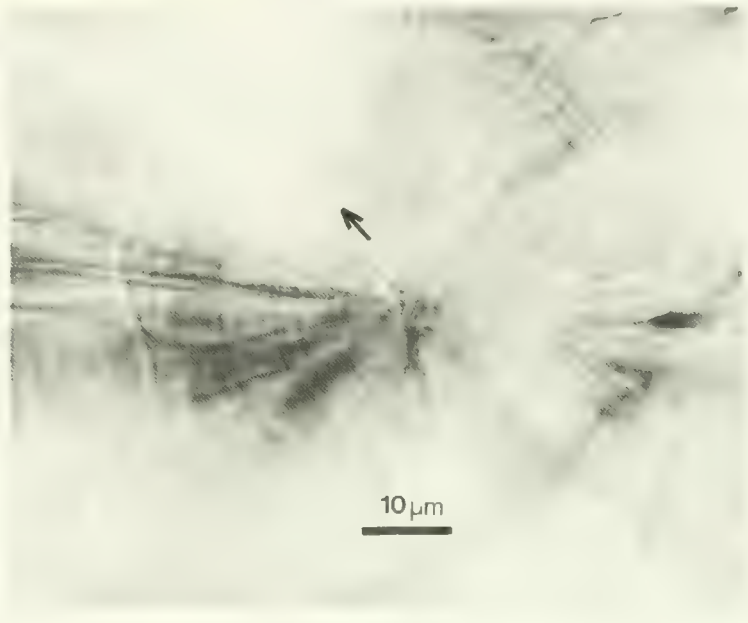

Figure 1
Photomicrograph of a shortbelly rockfish otolith showing the first increment (arrow) and subsequent development of increment microstructure.

Several lines of evidence indicate that the periodicity of otolith increments we counted was daily. For one, all back-calculated birthdate distributions fell within known annual parturition (spawning) seasons (Wyllie Echeverria 1987, MacGregor 1986). In addition, results from a separate study that sequentially sampled larval and juvenile shortbelly rockfish in 1989 showed that one increment was deposited each day from May to June (Laidig et al. In press). Lastly, Yoklavich and Boehlert (1987) validated the existence of daily growth increments in juvenile *S. melanops* using autoradiography to detect injected ^{45}Ca, as well as by tetracycline injection.

Under the assumption that one increment was produced each day, growth rate was measured by regressing SL (mm) against estimated age (days). Analysis of covariance was used to test for differences in the relationship of SL and age within and among years. When differences were found, pairwise comparisons of class means were made using the least significant difference (LSD) test (Snedecor and Cochran 1967). This test maintains the comparisonwise error rate at $\alpha = 0.05$, but, depending on the number of means compared, increases the experimentwise probability of committing a Type I error. In addition, indices of annual growth performance were obtained by predicting standard length at a selected standard age using regression statistics from each individual year. These were evaluated using principal component analysis (Green 1978) to reveal interdependency among the data. In this analysis, species were treated as variables, years comprised cases, and components were computed from the correlation matrix.

Back-calculated birthdate distributions of the fish that survived until the time of sampling were obtained by: (1) linearly regressing age on SL using the subsample of aged fish, (2) using the regression equation obtained to estimate the age of fish sampled during May–June cruises only, (3) back-calculating to the calendar date of first increment formation by differ-

ence (calendar date of capture minus age in days), and (4) aggregating the data into frequency distributions. Although with this approach some lengths were excluded, data from April cruises were not used due to the sporadic sampling (temporally and spatially) that occurred. Back-calculated birthdate distributions were compared within and among years, as well as among species.

Results

In some cases, analysis of covariance (ANCOVA) revealed statistically significant differences in the relationship of standard length and age among the various sweeps conducted within a year (i.e., bocaccio in 1987, chilipepper in 1988, widow rockfish in 1987, and yellowtail rockfish in 1986). It is notable, however, that these cases represented only 4 of the 15 species-year combinations for which data were available. Further examination of the data revealed that in one of these cases significance was due to a very small sample obtained during one sweep. Moreover, in the other three instances there was no regular pattern of either increasing or decreasing growth rate as the season progressed and the magnitude of differences was small. For these reasons a single regression equation describing the annual growth of each species was generated by pooling the age data obtained in a year, ignoring the sweep of origin.

Growth

Shortbelly rockfish There was a linear relationship between standard length (mm) and age (days) for shortbelly rockfish over the size range collected in each year during 1983–88 (Fig. 2). A simple linear growth model was fit to each year individually (Table 2). Annual estimates of pelagic juvenile shortbelly rockfish growth rate ranged from 0.524 mm/day in 1985 to 0.638 mm/day in 1983. Results from ANCOVA (Table 3) showed that significant differences (P 0.019) occurred in annual growth rates (i.e., slopes) among the six years sampled. Growth rates were relatively low in 1985 and 1986, were medium in 1984 and 1988, and were high in 1983 and 1987. To test for differences in estimates of annual growth rate, pairwise comparisons were made using LSD tests (Fig. 3).

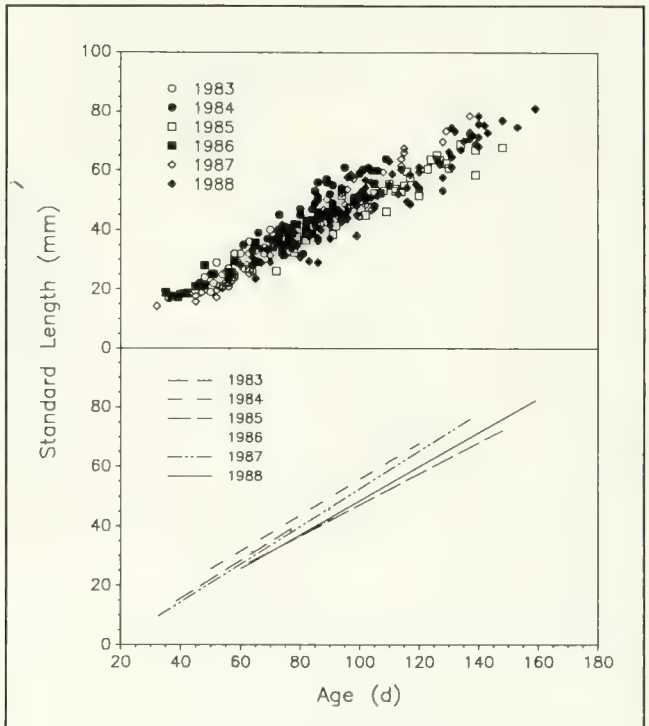

Figure 2
Scattergrams of shortbelly rockfish *Sebastes jordani* standard length on age for each year, 1983–88 (upper), with fitted linear regressions to each year of data (lower).

Table 2
Annual regression statistics for the linear growth model.

Rockfish species	Year	N	Slope (mm/d)	Slope (SE)	Intercept (mm)	Intercept (SE)	r^2
Shortbelly	1983	32	0.6377	(0.0650)	−9.7612	(3.9387)	0.763
	1984	52	0.6025	(0.0487)	−4.4985	(4.1709)	0.754
	1985	40	0.5239	(0.0258)	−5.3236	(2.7594)	0.915
	1986	34	0.5316	(0.0199)	−2.4195	(1.4332)	0.957
	1987	53	0.6349	(0.0183)	−10.9365	(1.6089)	0.959
	1988	91	0.5735	(0.0197)	−8.7806	(2.0927)	0.905
Bocaccio	1984	50	0.6774	(0.0382)	−16.8644	(3.9810)	0.868
	1985	19	0.9737	(0.1076)	−56.4082	(12.0249)	0.828
	1986	48	0.5627	(0.0226)	−11.2418	(1.7521)	0.931
	1987	90	0.7346	(0.0209)	−24.6335	(1.9917)	0.934
	1988	53	0.7339	(0.0449)	−30.7046	(5.5366)	0.840
Chilipepper	1985	36	0.4028	(0.0336)	−2.5392	(3.3381)	0.808
	1986	27	0.3990	(0.0365)	0.3622	(2.8803)	0.827
	1987	74	0.5553	(0.0190)	−9.9867	(2.0029)	0.922
	1988	74	0.5500	(0.0239)	−16.8179	(2.7082)	0.881
Widow	1985	25	0.5647	(0.0762)	−13.9356	(8.8497)	0.705
	1986	9	0.2986	(0.0978)	13.2109	(9.5706)	0.571
	1987	45	0.6070	(0.0316)	−13.4434	(3.0735)	0.896
	1988	49	0.5696	(0.0231)	−13.2175	(2.7276)	0.928
Yellowtail	1985	18	0.1944	(0.0830)	20.4415	(9.6333)	0.255
	1986	9	0.4634	(0.0263)	−6.3261	(2.2973)	0.978
	1987	23	0.4620	(0.0655)	−1.7767	(6.9320)	0.703
	1988	24	0.4016	(0.0353)	−1.9092	(3.7319)	0.855

Table 3

Analyses of covariance testing for differences in slopes and adjusted means (i.e., elevation) of annual (1983–88) linear growth curves for each of five species of pelagic juvenile rockfish. Tests for adjusted means were done only when the test of equality of slope was not significant. Dependent variable = SL, covariate = age, treatment variable = year.

Rockfish species Source	df	Sum of squares	Mean square	F	*P*
Shortbelly					
Equality of slopes	5	219.30	43.86	2.74	0.019
Error	290	4,637.14	15.99		
Bocaccio					
Equality of slopes	4	705.01	176.25	6.16	0.001
Error	250	7,157.92	28.63		
Chilipepper					
Equality of slopes	3	262.68	87.56	5.00	0.002
Error	203	3,557.01	17.52		
Widow					
Equality of slopes	3	75.63	25.21	1.64	0.184
Error	120	1,845.44	15.38		
Equality of adjusted means	3	392.41	130.80	8.38	0.001
Error	123	1,921.07	15.62		
Yellowtail					
Equality of slopes	3	57.41	19.14	2.13	0.104
Error	66	591.95	8.97		
Equality of adjusted means	3	798.09	266.03	28.27	0.001
Error	69	649.36	9.41		

Bocaccio The data presented in Figure 4 show the relationship between standard length and age for the aged subsamples of pelagic juvenile bocaccio in each year during 1984–88. No data were available for 1983. There is some suggestion of curvilinearity in the data, especially in the youngest stages of growth, but this cannot be confirmed due to annual differences in the age domain sampled. For example, specimens ranged in age from 35 to 113 days during 1986, whereas in 1985 they ranged from 84 to 131 days. Thus, differences in slope between these years may be due to a year effect in the linear model, or to violation of the linearity assumption. In spite of the suggestion of nonlinearity in the data when pooled over years, the linear model was used to conform with the analyses performed on the other four species studied and because it fits well on a year-by-year basis.

A simple linear growth model was fit to individual years (Table 2). During the period studied, the highest growth rate

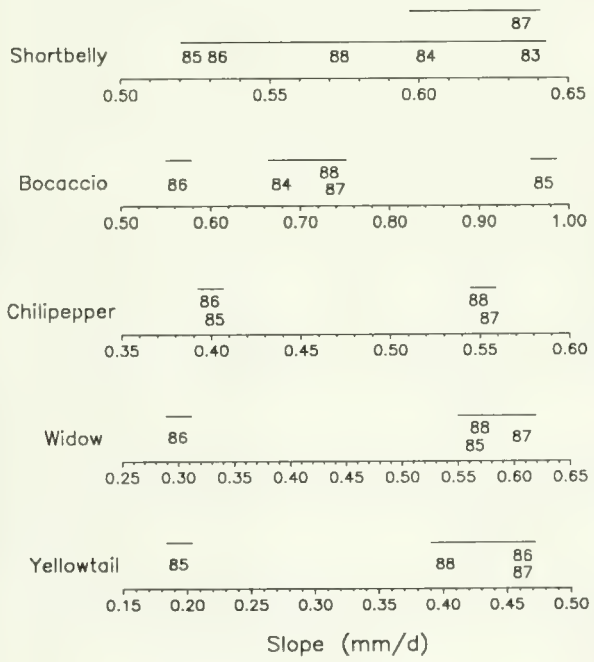

Figure 3

Results of all possible pairwise least-significant-difference tests of annual differences in growth rate (slope) for each species studied. A bar over and connecting different years (1983–88) indicates lack of significance. No adjustments were made to control the experiment-wide probability of Type I error.

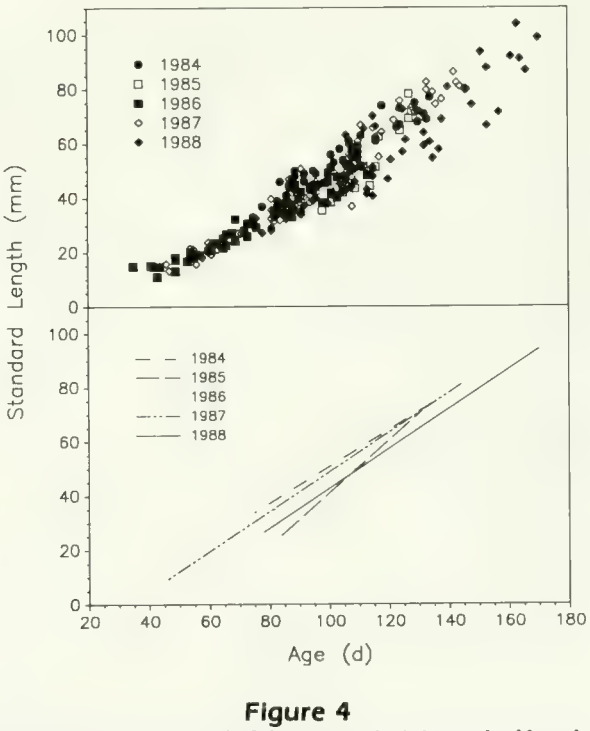

Figure 4

Scattergrams of bocaccio *Sebastes paucispinis* standard length on age for each year, 1984–88 (upper), with fitted linear regressions to each year of data (lower).

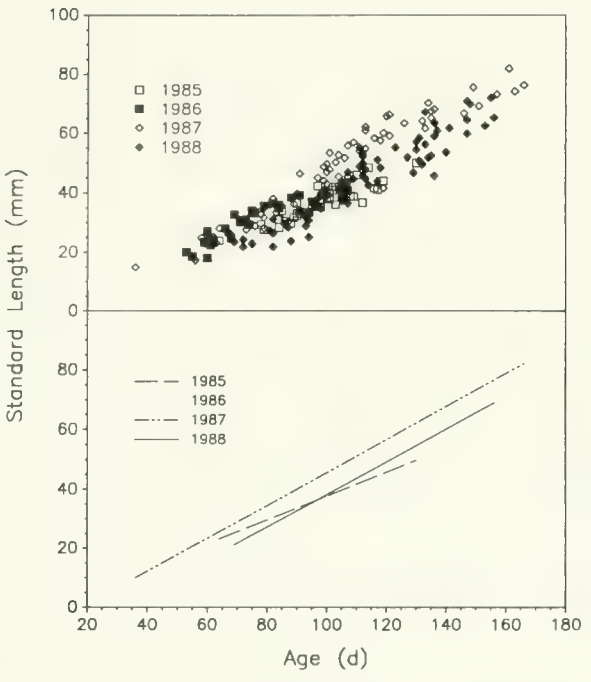

Figure 5
Scattergrams of chilipepper *Sebastes goodei* standard length on age for each year, 1985–88 (upper), with fitted linear regressions to each year of data (lower).

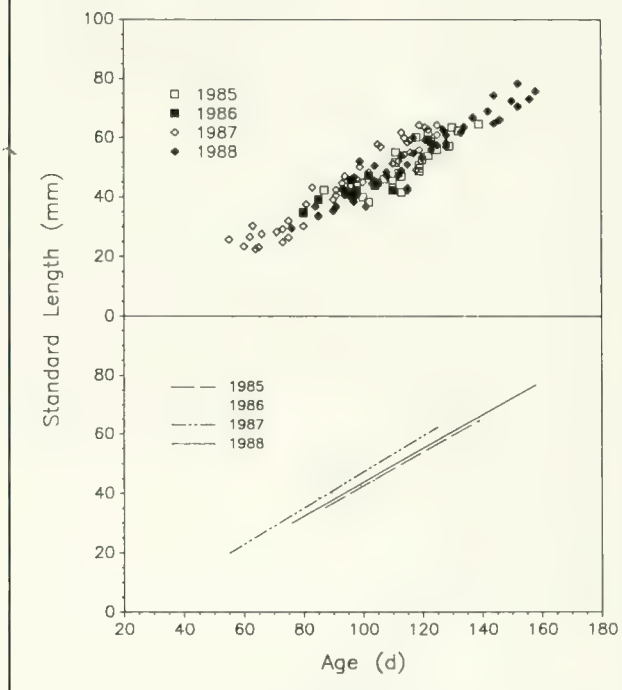

Figure 6
Scattergrams of widow rockfish *Sebastes entomelas* standard length on age for each year, 1985–88 (upper), with fitted linear regressions to each year of data (lower).

occurred in 1985 (0.974 mm/day), whereas the lowest growth rate (0.563 mm/day) was seen in 1986. Results of ANCOVA (Table 3) show that significant differences (P 0.001) in growth rate occurred among years. Results of all possible pairwise LSD tests comparing annual slope estimates (Fig. 3) show that growth in 1985 was distinctly fast. Growth rates were relatively low in 1986 and were moderate and similar in 1984, 1987, and 1988.

Chilipepper Sufficient numbers of fish were collected during 1985–88. Standard length and age data from these years (Fig. 5) indicate an apparent linear relationship. Regression statistics resulting from fitting each year's data to the linear growth model are provided in Table 2. Annual growth rates ranged from a low of 0.399 mm/day in 1986 to a high of 0.555 mm/day in 1987. Results from ANCOVA (Table 3) show that annual differences exist in growth rate (P 0.002); pairwise LSD comparisons of slopes (Fig. 3) indicate a very clear separation between the slow growth that occurred in 1985–86 and the relatively fast growth in 1987–88.

Widow rockfish Like chilipepper, widow rockfish were collected in sufficient numbers only in the years 1985–88. The scatter of data (Fig. 6) shows an apparently linear increase in standard length, at least over the range of ages sampled. A problem with the data is that in 1986 only 9 fish were collected, with ages ranging 80–110 days. This resulted in a marked reduction in age contrast (30 days).

The data from each year were fitted separately with linear regression (Table 2), with estimates of growth rate ranging from 0.299 mm/day in 1986 (N 9) to 0.607 mm/day in 1987. When ranked, the descending sequence of estimated annual growth rates (i.e., slopes) was: 1987>1988>1985>1986. Results of ANCOVA (Table 3), however, indicated that slopes did not vary significantly among years (P 0.184), although all possible pairwise LSD comparisons (Fig. 3) showed that growth rate in 1986 was slower than in other years. The reason the ANCOVA failed to reveal differences in slope among years was likely due to a small sample size and low age contrast in 1986. An F-test for annual differences in adjusted means (i.e., elevation) did reveal significant differences (Table 3, P 0.001). Pairwise LSD comparisons of annual adjusted means indicated that pelagic juveniles were larger in 1987 than in other years. When ranked, the descending sequence of annual adjusted means was: 1987>1986>1988 >1985.

Yellowtail rockfish Juvenile yellowtail rockfish comprised the fewest specimens collected of the five species studied. Sufficient specimens for growth analysis were collected only in the years 1985–88. The scattergram (Fig. 7) shows the smallest range in standard length and age observed. This problem is exemplified in 1985 when the ages ranged only 107–133 days.

The data were fitted by linear regression for each year (Table 2) resulting in estimates of growth rate that ranged from 0.194 mm/day in 1985 to 0.463 mm/day in 1986. The descending sequence of estimated annual growth rates of yellowtail rockfish was: 1986>1987 >1988>1985. Results of ANCOVA (Table 3) testing for annual differences in slope were borderline (P 0.104); all possible pairwise LSD comparisons (Fig. 3) showed that growth rate in 1985 was slower than in other years. An F-test of annual differences in adjusted means was significant (Table 3, P 0.001). Like widow rockfish, results from all possible pairwise comparisons of yearly adjusted mean standard length indicated that yellowtail rockfish juveniles were larger in 1987 than in other years, with fish sampled in 1986 and 1988 somewhat larger (P 0.05–0.10) than those taken in 1985. The rank order of adjusted mean standard length was identical to that observed in widow rockfish (i.e., 1987>1986>1988>1985).

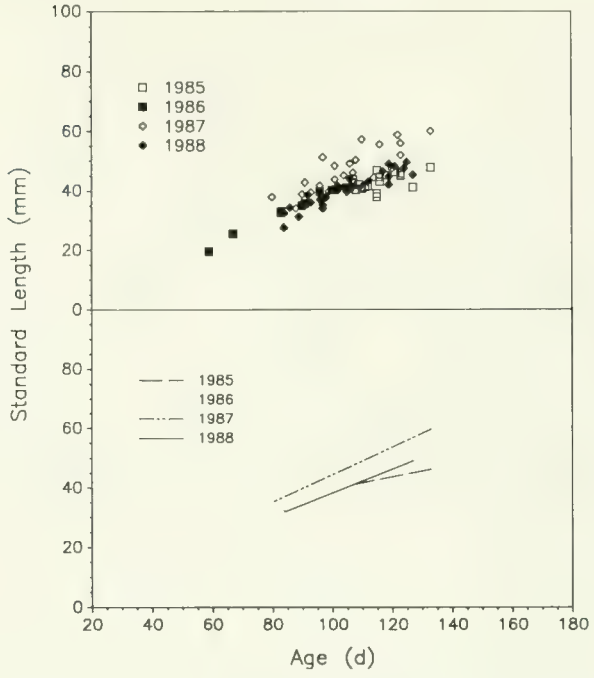

Figure 7
Scattergrams of yellowtail rockfish *Sebastes flavidus* standard length on age for each year, 1985–88 (upper), with fitted linear regressions to each year of data (lower).

Annual growth performance

The data presented thus far make it difficult to compare and contrast the growth of the five species on an annual basis. For example, results from bocaccio (lower panel in Figure 4) show that 1985 was characterized by the highest growth rate (0.974 mm/day). Even so, 90-day-old fish in 1985 were estimated to be smaller than in any other year. In this situation it is possible that poor growth performance during early-life-history stages, prior to those sampled, had no lasting effect on growth at the time of sampling. There may even have been some form of compensatory growth response.

To overcome this problem we compared annual growth performance within and among species by estimating length at a selected standard age with the regression statistics presented in Table 2. This is functionally equivalent to integrating annual growth rates up to the selected standard age, providing a common basis for comparison among years. The standard age for each species was determined from the range of ages sampled in the various years. Standard ages were selected to prevent extrapolation of the regressions. Specific ages selected were: shortbelly rockfish 70 days, bocaccio 100 days, chilipepper 90 days, widow rockfish 100 days, and yellowtail rockfish 107 days.

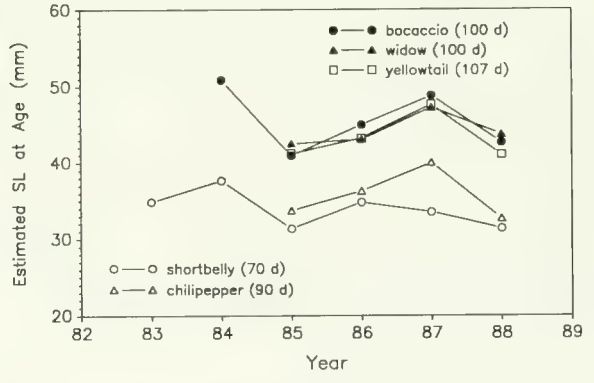

Figure 8
Annual estimates (1983–88) of standard length at standardized ages of shortbelly, bocaccio, chilipepper, widow, and yellowtail rockfishes.

Results show coherent differences in growth performance from year to year (Fig. 8). Among the five species over the last four years of the study, 1985 consistently produced the smallest fish and, with the exception of shortbelly rockfish, 1987 yielded the largest fish observed. Although only represented by two

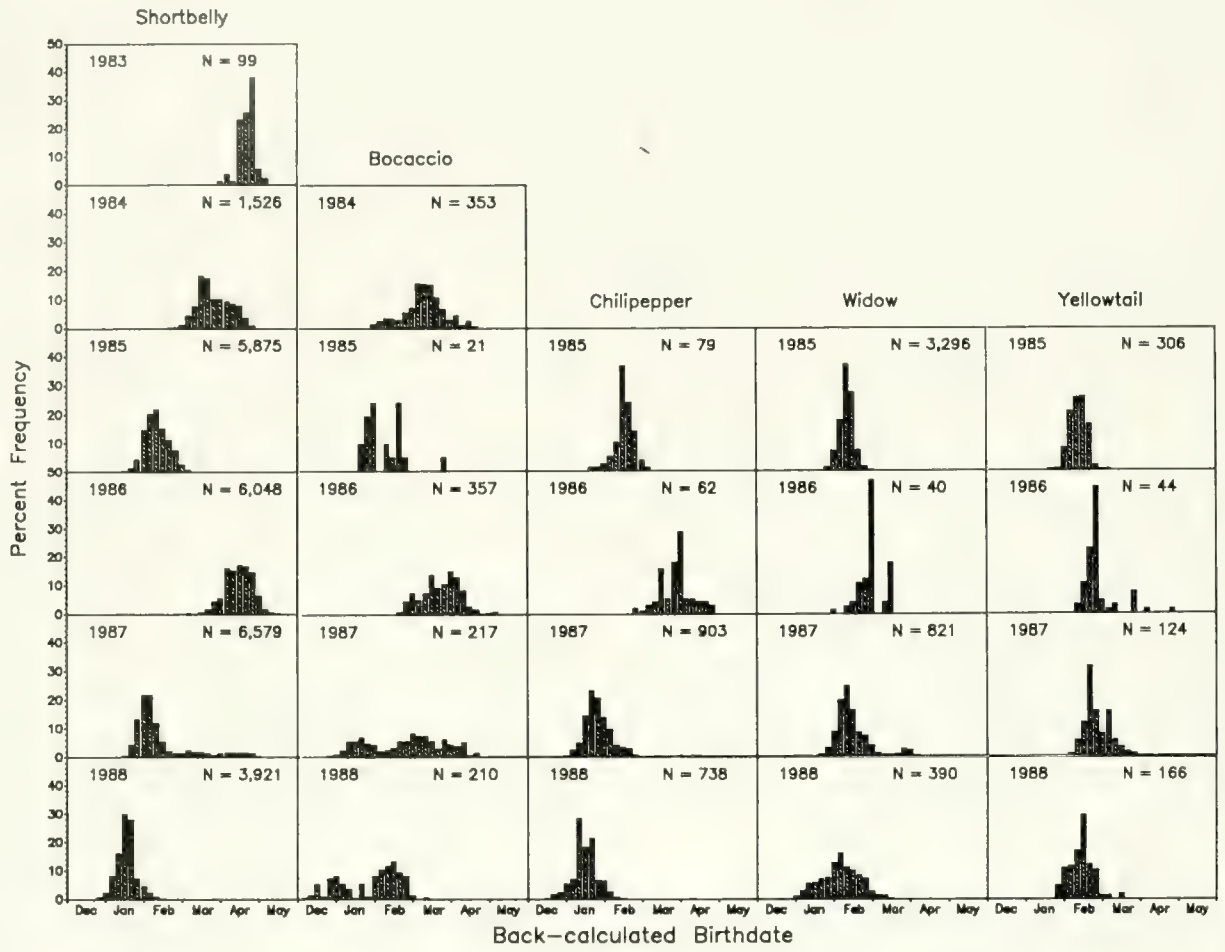

Figure 9

Composite annual back-calculated birthdate distributions of shortbelly, bocaccio, chilipepper, widow, and yellowtail rockfishes (1983–88).

species (bocaccio and shortbelly rockfish), 1984 produced faster growth than in any other year.

Overall, growth performance shows remarkable coherency in this time series. This conclusion is further reinforced with results from principal component analysis. Following ordination, 83.3% of the variation in growth-performance standard scores was accounted for by the first principal component (λ_1 4.16). First component scores (ξ_1) for each year were ranked in descending order as follows: 1987 (ξ_1 2.74)>1986 (ξ_1 0.36)>1988 (ξ_1 −1.40)>1985 (ξ_1 −1.71). These values follow the general pattern evident in Figure 8.

Back-calculated birthdate distributions

As with the aged subsample data, the birthdate frequency distributions that were generated from length-frequency data were pooled across sweeps within each year, even though in some cases significant differences occurred. Although sweep-to-sweep differences would be useful in elucidating within-season patterns of mortality, movement, and growth, we ignored them because an analysis of the components of variance showed that, with the exception of yellowtail rockfish, variation of this kind was quite minor in comparison to yearly fluctuations in birthdate distributions.

Results of back-calculating time of birth (Fig. 9) show that, typically, surviving juveniles were born during a two-month period. For most species-year combinations, a unimodal distribution is evident. Bocaccio display somewhat broader birthdate distributions than the other species, perhaps reflecting their multiple spawning capability in southern California waters (MacGregor 1970). Positive skewness in the birthdate

distributions of all five species was evident in 1987, being particularly marked in shortbelly, chilipepper, and widow rockfish. What is most striking in these data, however, is the broad coherence among the species in the yearly shifts that occurred in the distributions (Fig. 10). For example, 1986 was a year in which successful parturition occurred late in the season for all species examined. Conversely, 1985 and 1988 were years marked by earlier birthdate distributions.

Principal component analysis demonstrates the great degree to which these data are coherent in time (1985–88). Results show that 92.9% of the variation in mean back-calculated calendar birthdate standard scores was accounted for by the first principal component (λ_1 4.64). Given the tight coupling that occurred between bocaccio and shortbelly rockfish in 1984–85, these values may well have been higher if data had been available for all species in all years (1983–88). First component scores for each year were ranked in descending order as follows: 1986 (ξ_1 2.93)>1987 (ξ_1 0.13)>1985 (ξ_1 −1.16)>1988 (ξ_1 −1.89). This sequence mirrors the interannual shifting of distributions evident in Figures 9 and 10.

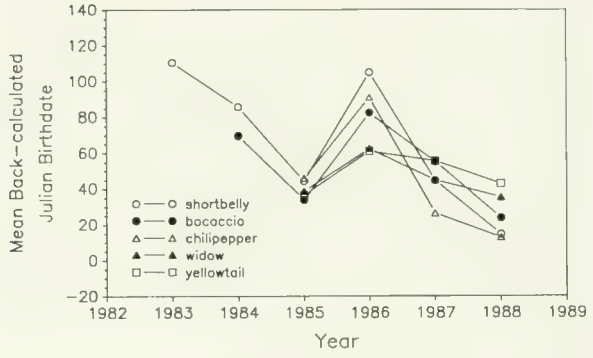

Figure 10

Annual trends (1983–88) in the means of back-calculated birthdate distributions for shortbelly, bocaccio, chilipepper, widow, and yellowtail rockfishes.

Discussion

Growth

Growth rates of field-collected larval and pelagic juvenile *Sebastes* spp. have been determined by others using otolith microstructure (reviewed in Kendall and Lenarz 1987, Moser and Boehlert 1991). It is noteworthy that in all cases a linear growth model fitted the data best, similar to results reported here (Figs. 2, 4–7). Data for *S. melanostomus* (*N* 4) indicated that at 15–30 mm SL the growth rate was 0.24 mm/day (Moser and Ahlstrom 1978). Research on *S. diploproa* (Boehlert 1981) showed a growth rate of 0.19 mm/day for fish 10–40 mm SL. Both studies were conducted off southern California. Penney and Evans (1985) estimated that redfish (composite of *S. marinus*, *S. mentella*, and *S. fasciatus*) from the northwest Atlantic grew at the rate of 0.11–0.16 mm/day when in the range 8–25 mm TL.

These growth rates are somewhat lower than those presented in Table 2. Our data show growth rates ranging 0.52–0.64 mm/day for shortbelly rockfish, 0.56–0.97 mm/day for bocaccio, 0.40–0.56 for chilipepper, and 0.30–0.61 mm/day and 0.19-0.46 mm/day for widow and yellowtail rockfishes, respectively. This is likely due to the span of ages and/or sizes caught, since our fish were larger and older than in these other studies. It is conceivable, however, that the growth rates of pelagic juvenile *Sebastes* spp. along the central California coast are enhanced in response to superior feeding conditions and increased ration (Brett 1979), a consequence of elevated production associated with coastal upwelling (Smith 1968). Dietary studies of these fishes show that they feed primarily on various life stages of euphausiids and calanoid copepods (Reilly et al. In prep.).

Interannual variation in growth performance has been implicated as a major factor affecting year-class strength (Miller et al. 1988). Houde (1987) showed with simple calculations that, in some situations, a doubling of the instantaneous growth rate during the early life history can increase the number of recruits by nearly 100-fold. Moderate and significant interannual variations in growth rates/performance were evident for the species in this study. Likewise, widow rockfish year-class strength has varied 10-fold during the 1974–89 period (Hightower and Lenarz 1989). These results are, therefore, consistent with the hypothesis that fluctuations in rockfish recruitment are due, at least in part, to interannual variation in growth rate.

Birthdate distributions

Back-calculation of birthdate distributions using daily increment data has been reported before (e.g., Bolz and Lough 1983, Brothers et al. 1983, Methot 1983, Jones 1985, Penney and Evans 1985, Thorrold 1989). One difficulty with this approach is that estimates of the numbers born by date should be adjusted for differences in mortality (Penney and Evans 1985), i.e., to have appeared in our samples, older juveniles must have survived for a longer period of time than younger ones. However, without an estimate of early larval and juvenile mortality rates we were unable to adjust for

this effect. In this sense, the histograms presented in Figure 9 represent the birthdate distributions of the fish that survived to the time of sampling.

The distributions are also influenced by other factors. For example, there are differences among the species in duration of the pelagic phase. This is especially true for widow and yellowtail rockfish, which tend to settle at a relatively young age. Results may also be biased if parturition occurs unusually late in the year. In this case the larvae/juveniles might not be large enough to be captured by the gear we used. However, our sampling occurred annually at similar times, and marked differences in the distributions were still noted. The early birthdate distributions characterizing bocaccio, chilipepper, and shortbelly rockfish in 1988 were due to the prevalence of relatively old fish, whereas fish sampled in 1986 were relatively young. Although these shifts may be influenced by settlement and gear selectivity, they nonetheless provide a conservative representation of interannual differences.

Two possible hypotheses accounting for interannual variation in the means of back-calculated birthdate distributions are (1) annual variation in the seasonal timing of parturition, and (2) year-specific seasonal variation in the expression of mortality rates within fixed parturition seasons. Although at present we have no basis to distinguish between these two alternatives, this topic is currently under detailed investigation.

Oceanographic conditions

It is well known that temperature has a major influence on larval growth at sea. There is evidence that sea-surface temperature (SST) affects the growth performance of pelagic juvenile rockfish off central California (lat. 36–39°). In this area mean January SST from 1983–87 (Cole and McLain 1989) was positively associated with growth performance. For example, in 1984 shortbelly rockfish were estimated to be 37.7 mm SL at a standard age of 70 days. This represented this species' best growth during the 1983–88 period, and in this year mean January SST was a very warm 13.12°C. In contrast, in 1985, when mean January SST was at its lowest value in the time series (12.05°C), estimated length at age was lowest also (31.3 mm SL).

Similar to growth, there is evidence that sea-surface temperature has a strong influence on interannual shifting of back-calculated birthdate distributions. Cold years were associated with early successful parturition. Our results show that for shortbelly rockfish the annual mean of the birthdate distribution was at its minimum in 1985 (8 February) when mean January SST was only 12.05°C. By comparison, in 1983 (an El Niño year) the birthdate mean was at its maximum value (21 April) in association with warm January SST (13.16°C). These findings are intriguing and form the basis of ongoing investigations into the establishment of year-class strength in *Sebastes* spp.

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A Larva of the Poorly Known Serranid Fish *Jeboehlkia gladifer* (Teleostei: Serranidae: Epinephelinae)*

Carole C. Baldwin

Virginia Institute of Marine Science, School of Marine Science
College of William and Mary, Gloucester Point, Virginia 23062

G. David Johnson

Division of Fishes, National Museum of Natural History
Smithsonian Institution, Washington, D.C. 20560

Jeboehlkia gladifer Robins, 1967, was described from a single mature female collected at 165 m (90 fm) in the Caribbean Sea. Several additional specimens have been collected recently in similarly deep waters of the Caribbean and western North Atlantic (R.G. Gilmore, Harbor Branch Found., Ft. Pierce, FL, pers. commun., Fall 1990). Robins (1967) noted a strong resemblance between *J. gladifer* and the epinepheline genus *Liopropoma*, but accorded the former generic status on the basis of absence of pored lateral line scales. Several features of the holotype—its small size (40.8 mm standard length, SL), elongate dorsal fin spine, produced pelvic fin rays, and large eye—appear paedomorphic with respect to other epinephelines (Kendall 1984).

The following description of larval *Jeboehlkia* is based on a single specimen, 10.2 mm SL, collected between 10 and 300 m in Atlantic slope water off New York (MCZ 81740, Fig. 1). The specimen is in poor condition, lacks pigment (but possibly it is naturally unpigmented), and is bent in half at midbody; nonetheless, it is identifiable as *J. gladifer* on the basis of counts and morphology of fin rays. The holotype (USNM 201422) has the following counts: dorsal fin rays VIII,9; anal fin rays III,7; pectoral fin rays 15; pelvic fin rays I,5; principal caudal fin rays 17 and vertebrae 24. The spinous dorsal fin in the larval specimen is incomplete, but the larva clearly has nine dorsal-fin soft rays, a meristic feature unique among Atlantic Epinephelinae to *Jeboehlkia* (see Kendall 1979, Table 1). Corroborating the identification of this specimen as *Jeboehlkia* is the presence of seven anal-fin soft rays, 15 pectoral fin rays, and a thin, flexible, elongate second dorsal fin spine. Although Robins (1967) stated that the holotype has seven dorsal-fin spines and that the first spine is the elongate element, an examination of a radiograph of the holotype indicates that the first spine is only an unexposed nubbin and was overlooked by Robins; consequently, there is a total of eight (not seven) dorsal-fin spines. The tiny first spine is the only element borne in supernumerary association with the first dorsal fin pterygiophore, and the elongate (second) spine in larval *Jeboehlkia* is serially associated with the first dorsal pterygiophore, a hallmark of all known larvae of the Epinephelinae.

The specimen was illustrated (flattened right-side-up beneath a glass microscope slide) with the aid of a camera lucida and then photographically reversed. The pectoral fin was drawn from the left side of the body, and myomeres were reconstructed from a combination of vertebrae (partially visible on the damaged right side of the body) and myomeres (partially visible on the left side of the body). Counts, measurements, and qualifications of morphometric features (e.g., moderately deep, large) follow Leis and Trnski (1989). Standard length is abbreviated as SL; institutional acronyms are as listed in Leviton et al. (1985).

The postflexion larva of *J. gladifer* is laterally compressed, moderately deep (body depth at pectoral fin base 34.5% SL), and has a large head (42.4% SL). The specimen essentially is eviscerated, but the anus is evident just posterior to midbody (56.5% SL). The eye is round, moderately large, and greater in diameter than the length of the snout (diameter of eye 11.0% SL, length of snout 9.4% SL). The mouth is large, the maxilla reaching just beyond middle of the eye.

The distance between the dorsal and ventral body margins of the caudal peduncle is 15.7% SL (between dashed lines on caudal peduncle in Figure 1), but the total depth of the peduncle is greater (18.6% SL between solid lines on caudal peduncle in Figure 1). This disparity is due to the presence of two blade-like sheaths of modified tissue that lie above and below the dorsal and ventral margins of the caudal peduncle, respectively, and extend from the posterior bases of the dorsal and anal fins to the caudal fin. This tissue contains numerous small globules (of fat?). Tissue with a similar appearance covers the procurrent rays of the caudal fin and appears along the lengths of most principal caudal fin rays, on the rays of the soft dorsal and anal fins, and on the head.

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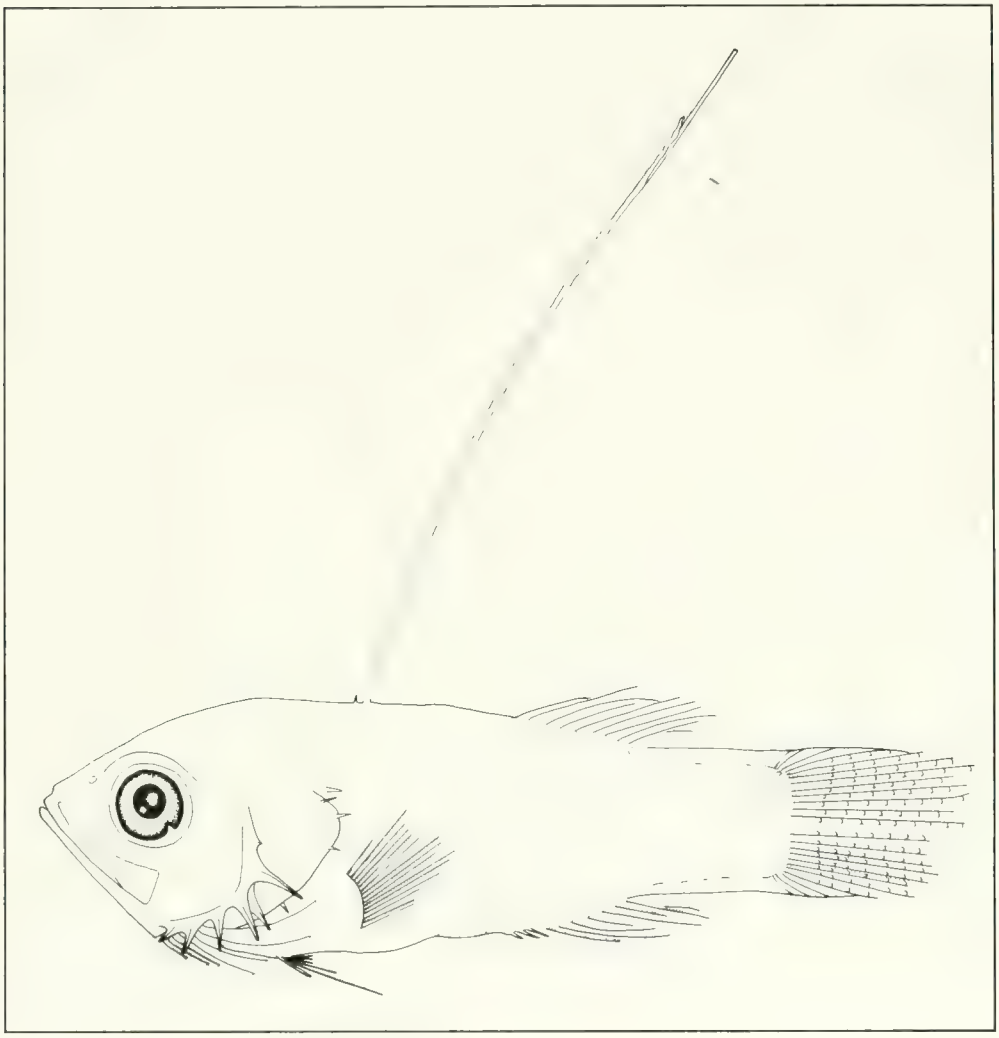

Figure 1
Larva of *Jeboehlkia gladifer*, MCZ 81740, 10.2mm SL, collected in the western North Atlantic Ocean (40°42.0′N, 65°00.3′W).

The longest ray of the pectoral fin measures 15.1% SL, but all rays appear broken, and the original length of the fin is unknown. Pelvic fin rays also appear broken, but the first soft ray on the right side and second on the left side are clearly produced. Robins (1967) noted that the first two pelvic rays are very elongate in the holotype, and both are probably elongate in intact larvae.

The elongate second dorsal-fin spine is thin, flexible, and covered with a sheath of tissue that is torn distally. It measures 105% SL but is broken, and we are unable to determine its original length.

There is a full complement of soft dorsal (9), anal (III,7), pectoral (15), and principal caudal fin rays (9+8). Only the first two dorsal fin spines are visible externally, but four additional tiny spines that have not yet emerged through the skin are apparent in a radiograph of the larva. The procurrent caudal fin rays are difficult to see, but the specimen appears to have three in both the dorsal and ventral caudal lobes, two fewer than the adult complement of 4+4, as determined from a radiograph of the holotype. The pelvic fin bears one spine and five soft rays, the medialmost two of which are closely approximated. All fin spines are smooth.

There are six prominent smooth preopercular spines, the four on the lower limb becoming increasingly antrorse anteriorly. Robins (1967) noted the presence of three strong antrorse spines on the lower limb of the preopercle in the holotype. Our examinations indicate that the three anteriormost antrorse spines in the larval specimen are very similar in morphology and position to those of the holotype and thus provide additional corroborative evidence for the identification of the larval specimen as *J. gladifer*. Antrorse preopercular spines are rare among larval epinephelines (present in some larvae of the epinepheline tribe Epinephelini, Leis 1986), and their presence in larval *J. gladifer*, in combination with other characters, appears diagnostic. The interopercle and supracleithrum each bear one well-developed smooth spine, and a

single small spine is present on the subopercle; spines are lacking on the lateral ridge of the preopercle and supraorbital ridge of the frontal. The frontal bones bear a conspicuous "golf ball-like" pattern of very small pits (not illustrated in Figure 1), not nearly so prominent as the raised network of ridges (rugosity) found in some anthiine and epinephelin serranids. Scales are lacking and presumably have not yet formed.

The relationship of *Jeboehlkia* to other Epinephelinae is unclear. Robins (1967) regarded it as a close relative of *Liopropoma*. Johnson (1983), following Robins, included it in his tribe Liopropomini, but did not examine the holotype. The presence in larval *Jeboehlkia* of a single (vs. two in *Liopropoma*) elongate filamentous dorsal fin spine, robust (vs. weak) spines on the medial preopercular ridge, and absence (vs. presence) of spines on the lateral preopercular ridge suggest affinities with Johnson's (1983) Grammistini (see Baldwin et al. 1991), and some aspects of adult morphology corroborate this. A cladistic analysis of epinepheline genera based on larval and adult morphology, which should elucidate the proper phylogenetic placement of *Jeboehlkia*, is in progress.

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Apparent Predation by a White Shark *Carcharodon carcharias* on a Pygmy Sperm Whale *Kogia breviceps*

Douglas J. Long

Department of Integrative Biology and the Museum of Paleontology
University of California, Berkeley, California 94720

The white shark *Carcharodon carcharias* is one of the largest predatory fishes in the world's oceans, and is an important apex predator in coastal waters. The diet of the white shark is quite diverse, including bony fishes, sharks, sea turtles, birds, and various invertebrates (Compagno 1984). Adults prey frequently on marine mammals. In the northeast Pacific, white sharks kill and eat sea lions *Zalophus californianus* and *Eumetopias jubatus*, elephant seals *Mirounga angustirostris*, and harbor seals *Phoca vitulina* (Ainley et al. 1981 and 1985, Le Boeuf et al. 1982, McCosker 1985), and are known to kill sea otters *Enhydra lutris*, although none have been found in the stomachs of the sharks (Ames and Morejohn 1980). In other oceans, there are several records of white shark predation on cetaceans, specifically on the harbor porpoise *Phocoena phocoena* and the bottlenose dolphin *Tursiops truncatus* (Arnold 1972, Corkeron et al. 1987), but the majority of accounts are largely anecdotal. There are few published records of white sharks attacking larger cetaceans, and no published records of white sharks in the northeast Pacific attacking cetaceans. Of over 100 white sharks collected in California waters between 1935 and 1984, the ones whose stomach contents were examined were not known to have the remains of any cetacean (Klimley 1985).

However, many authors (Randall 1973, Ellis 1975, Carey et al. 1982, Pratt et al. 1982, McCosker 1985) observed or documented white sharks scavenging on large whale carcasses off Australia and the eastern United States, and Castro (1983) suggested that whale carcasses may be a primary food resource for these sharks in some areas. To date, there is no documentation of white sharks preying or attempting to prey on a live cetacean other than a porpoise or dolphin. This study reports such predation and provides new information on the diet and predatory behavior of white sharks.

On 31 August 1989, a live pygmy sperm whale *Kogia breviceps* stranded at Pajaro Dunes beach north of Monterey near Watsonville in northern California. The whale, a 1.8 m, 82 kg male, was taken to the Long Marine Laboratory at the University of California, Santa Cruz, where it was kept alive for several weeks. I was able to examine and photograph the whale 18 days after the initial stranding, and noticed a pair of crescentric rows of gashes and punctures on the dorsal and ventral surfaces of the whale's body anterior to the caudal peduncle (Fig. 1). On the dorsal surface, the scars were narrow, parallel grooves that punctured the dermal layer and cut down into the muscles in several spots. The scars cut much deeper on the ventral surface: the anterior scars were deep puncture wounds, and the posterior scars were vertically-oriented parallel gashes that penetrated well into the muscle mass. The dorsal surface was penetrated by 12 teeth and the ventral surface by 9 teeth.

The shape and orientation of these scars strongly suggests that they were inflicted by a large predator in an attempt to capture the pygmy sperm whale. The size, shape, width, spacing, and orientation of these scars indicated that they were caused by a medium-to-large white shark, and the bite marks on the *Kogia* are different than those that could be made by other large sharks from northern Californian coastal waters such as the blue shark *Prionace glauca*, the short fin mako shark *Isurus oxyrinchus*, or the salmon shark *Lamna ditropis*. The only other sharks known to prey upon cetaceans are the tiger shark *Galeocerdo cuvieri* and large individuals of the genus *Carcharhinus* (Compagno 1984, Corkeron et al. 1987). These species are almost never seen in northern California waters (Compagno 1984), and the bite marks on the *Kogia* do not appear to have been made by these sharks. These conclusions are supported by comparisons with similar marks and injuries attributed to white sharks on pinnipeds and dolphins, and by comparisons with *C. carcharias* and jaws of other large predatory sharks examined by the author. Lastly, white sharks are frequently sighted and caught in the Monterey Bay area (Klimley 1985).

Observations on and documentation of white shark attack behavior by Tricas and McCosker (1984) also implicate *C. carcharias* as the attacker. First, white sharks usually attack their prey in a swift initial bite from below, behind, or from the side; the bite marks on the pygmy sperm whale are on the left, rear side of the body. Next, in the initial attack the shark opens its mouth by raising the head, dropping the lower jaw, and then thrusting it up into the prey while the upper jaw closes down. The shark will roll or shake

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Figure 1
Left lateral view of bite scars from a white shark *Carcharodon carcharias* on the anterior caudal peduncle of a live 1.8m juvenile male pygmy sperm whale *Kogia breviceps*. Dorsal scars correspond to the upper jaw of the shark, and ventral scars correspond to the lower jaw.

violently to inflict a fatal initial bite. The bite marks on the ventral surface of the whale were deeper than the dorsal set of scars, and the deepest scars were on the upper left and lower right, indicating initial penetration with the lower teeth, biting down of the upper jaw, and a roll to the left as the shark attacked the whale. The initial bite was relatively superficial and apparently unsuccessful, since the whale survived the attack. The bite-and-spit attack behavior of the white shark (McCosker 1985, Tricas and McCosker 1984) may have allowed the whale to escape any further injury by the same shark.

Many white shark attacks are made while the prey is floating or swimming at the surface, and the shark usually attacks from below or behind (McCosker 1985). Pygmy sperm whales have been observed floating quietly on the surface of the ocean with the tail hanging low in the water (Caldwell and Caldwell 1989). This 'basking' behavior seen in Kogia may facilitate easier attack by predators.

Although shark predation on smaller odontocetes is apparently rare, white sharks are known to attack and eat living dolphins (Arnold 1972, Corkeron et al. 1987). White sharks are also known to eat marine mammals as large as adult male elephant seals. Le Boeuf et al. (1982), documented remains of a 3m-long male elephant seal that may have weighed over 600kg taken from the stomach of a 4.7m white shark. Thus, a 1.8m, 82kg whale is within the size range of white shark prey.

Based on calculations by Randall (1973), the width of the bite marks on the pygmy sperm whale (roughly 25cm wide) and the relative spacing between individual tooth scars indicate a 4–5m shark made them. Pratt et al. (1982) recorded white sharks 4–5m-long feeding on the carcass of a dead fin whale *Balaenoptera physalus*, and Le Boeuf et al. (1982) examined seven white sharks ranging in length from 2.4 to 5.5m and recorded pinniped remains in each of their stomachs. Therefore, medium and large white sharks attack and consume marine mammals their size or smaller, and scavenge on cetacean carcasses larger than themselves (Klimley 1985, McCosker 1985, Pratt et al. 1982).

This is the first report of an attack on a *Kogia*, and on any cetacean in the northeast Pacific by a white shark. It is one of the few records of a shark attack on a live cetacean, other than a porpoise or dolphin. In a recent review, Caldwell and Caldwell (1989) list no known predators for *Kogia*; this observation implicates white sharks as a predator.

Although such predation has not previously been reported, the ranges of white sharks and *Kogia* overlap in the coastal areas of eastern and western North

America, southeastern and southwestern South America, northwestern Europe, northwestern and southern Africa, southern Australia and New Zealand, and northeast Asia and Japan (Caldwell and Caldwell 1989, Compagno 1984). Therefore, other incidents of predation may be observed in these areas.

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Scientific Editor
Dr. Linda L. Jones
National Marine Mammal Laboratory
National Marine Fisheries Service, NOAA
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Publications Awards 1988-89

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The Publications Advisory Committee of the National Marine Fisheries Service is pleased to announce the awards for best publications authored by NMFS scientists and published in the *Fishery Bulletin* volume 87 and *Marine Fisheries Review* volume 50. Eligible papers are nominated by the Fisheries Science Centers and Regional Offices and are judged by the NMFS Editorial Board. Only articles which significantly contribute to the understanding and knowledge of NMFS-related studies are eligible. The following were deemed the best.

Fishery Bulletin 1989

Wallace W. Morse

Catchability, growth, and mortality of larval fishes. *Fishery Bulletin* 87: 417-446. Dr. Morse is with the Sandy Hook Laboratory, Northeast Fisheries Science Center, Highlands, New Jersey.

Marine Fisheries Review 1988

Kenneth N. Baxter, Carlton H. Furr Jr., and Elizabeth Scott

The commercial bait shrimp fishery in Galveston Bay, Texas, 1959-87. *Marine Fisheries Review* 50(2):20-28. Dr. Baxter, Dr. Furr, and Ms. Scott are with the Galveston Laboratory, Southeast Fisheries Science Center, Galveston, Texas. Dr. Furr has since retired from his position with the National Marine Fisheries Service.

Abstract.–Northern shrimp *Pandalus borealis* carapace length-frequency data collected from shrimp surveys and commercial catches between 1972 and 1986 were studied to estimate age, growth, and mortality in Pavlof Bay, Alaska. Dominant size modes representing 1971 and 1975 year-classes were separated from carapace length-frequency distributions by the use of a maximum-likelihood separation technique. The growth rate for the 1975 year-class was significantly greater than that of the 1971 year-class. Because the abundance of the 1975 year-class was lower than that of the 1971 year-class, an inverse relationship of growth to year-class strength was suggested. Age-at-sex transition appears to be related to year-class abundance or overall density as 1975 year-class shrimp completed transition at a younger age than that of 1971. Increases in natural mortality occurred after the 1971 year-class completed transformation to the female sex at age 6.4, and may indicate a combination of spawning stress and senescence or increasing abundance of the predator, Pacific cod *Gadus macrocephalus*. Dynamic pool yield-per-recruit analysis indicated maximum biomass of year-classes was achieved at or prior to full recruitment to the survey and commercial fishing gear. Because mortality rates are high, yield-per-recruit is optimized by harvesting more of the smaller male shrimp.

Manuscript accepted 5 July 1991.
Fishery Bulletin, U.S. 89:541–553 (1991).

Age, Growth, and Mortality of the Northern Shrimp *Pandalus borealis* Kröyer in Pavlof Bay, Alaska

Paul J. Anderson

Kodiak Laboratory, Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 1638, Kodiak, Alaska 99615-1638

The Alaska Peninsula region of the western Gulf of Alaska was the site of one of the world's major shrimp fisheries in the 1970s (Anderson and Gaffney 1977). A significant decline in shrimp abundance starting in 1978 lead to the closure of most areas to fishing in 1979, and to date the fishery has yet to reopen. The cause of this decline and the failure of stocks to recover to fishable levels are obscured by a lack of information on the population dynamics of pandalid shrimps in the western Gulf of Alaska. In an effort to fill this information gap, I have estimated the age, growth, and mortality of two year-classes from a stock of northern shrimp *Pandalus borealis* Kröyer, the major commercial species in the region.

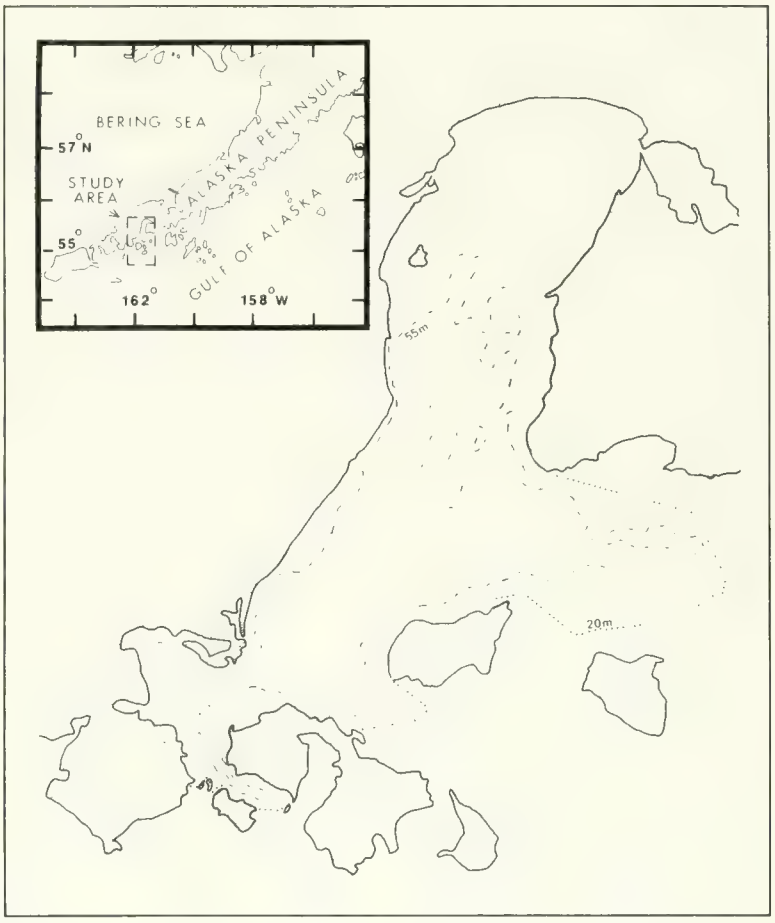
The Pavlof Bay (Fig. 1) stock of *P. borealis* was chosen for this study because it has supported a major fishery and an extensive database was available. The Bay was a major producer accounting for over 13,000 metric tons (t) of pandalid shrimp landings in 1977 alone. *Pandalus borealis* made up 11–97% of landings, with variable quantities of *P. goniurus*, *P. hypsinotus*, and *Pandalopsis dispar* making up the remainder. Pavlof Bay shrimp have been surveyed annually by the National Marine Fisheries Service (NMFS) since 1972. Data collected from these surveys include weight, number, and carapace length-frequencies by sex for *P. borealis*. The Alaska Department of Fish and Game (ADF&G) has collected species and size-composition data from commercial landings since the beginning of the fishery in 1968.*

Pandalus borealis in Pavlof Bay are managed as a discrete stock by the ADF&G. Analysis of data from commercial catches and shrimp surveys conducted by NMFS and ADF&G suggest that migration between adjacent bays along the Alaska Peninsula is minimal (Jackson et al. 1983). Vertical migrations in concert with ocean currents may act as dispersal mechanisms for pandalids (Barr 1970, Pearcy 1970, Gotshall 1972). In Pavlof Bay, effects of ocean currents probably are minimized by barrier islands and shallow entrances that favor confinement and limit immigration (Fig. 1).

Since there are no known anatomical structures for ageing *P. borealis*, researchers have used length-frequency analysis to estimate age and growth. For example, Rasmussen (1953) used dominant year-class modes to interpret growth and sex transformation of *P. borealis* in Norwegian stocks, and Skúladóttir (1981) used the positive deviations from long-term length-frequency distributions to identify average lengths-at-age for *P. borealis* from Icelandic fjords.

* Commercial landings, species, and size composition data available from Alaska Department of Fish and Game, 211 Mission Road, Kodiak, AK 99615.

Figure 1
Pavlof Bay, Alaska, sampling area showing 55 m isobath (dotted/dashed line) and approximate location of the 20 m isobath (dotted).



I have separated the dominant size modes representing year-classes from Pavlof Bay length-frequency distributions using the maximum-likelihood technique of Macdonald and Pitcher (1979). Annually, calculated mean lengths and numerical abundance of year-classes were then used to estimate growth and mortality using methods similar to those of Fréchette and LaBonté (1981) and Anderson (1981). The present study expands on previous work by using modal analysis of length-frequencies from commercial catches to estimate fishing and natural mortality rates. Results from these analyses were used to examine the yield-per-recruit function in relation to mortality and growth as well as year-class strength.

Materials and methods

Pavlof Bay was surveyed annually from 1972 to 1986 by trawling at randomly selected stations from August to mid-September (Table 1). During these months dense aggregations of *P. borealis* form in relatively deep water prior to mating and spawning. Earlier surveys had shown that shrimp concentrate in depths greater than 70 m (Ronholt 1963). Consequently, all survey tows were restricted to depths greater than 55 m (Fig. 1). Each year, except 1973, 10 to 13 randomly selected (with replacement) locations were chosen from a grid of the Bay's shrimp habitat divided into 22 stations (~13.7 km^2 each). Sampling was conducted with a 30-minute tow (~1.8 km) during daylight using a 32 mm mesh (32 mm mesh codend liner) high-opening shrimp trawl with an 18.6 m headrope and footrope (Wathne 1977). The mesh size and configuration of this trawl were similar to commercial fishing gear which allowed for direct comparison between survey and commercial data.

Carapace lengths (CL) were measured to the nearest 0.5 mm (eye socket to midposterior carapace edge) for approximately 300 specimens of *P. borealis* selected at random

Table 1
Biomass estimates and commercial landings (catch) of *Pandalus borealis* shrimp in Pavlof Bay, 1972–86 (metric tons with 80% confidence intervals for biomass; catches removed prior to next research survey).

Dates	No. tows	Biomass[1] (mt)		Catch[2] (mt)
7–10 Sep 1972	10	8,310	(6,999–9,616)	177
13 Sep 1973[3]	2	3,084	(3,062–3,107)	1,075
8–10 Sep 1974	13	11,476	(10,406–12,546)	150
19–21 Sep 1975	12	6,886	(5,597–8,174)	1,919
12–14 Sep 1976	12	10,796	(9,086–12,501)	5,670
25–27 Aug 1977	13	12,392	(9,462–15,318)	3,819
29–30 Aug 1978	13	3,602	(2,880–4,323)	826
4–7 Sep 1979	10	599	(367–830)	Closed
24–26 Aug 1980	12	549	(376–721)	Closed
10–11 Sep 1981	12	662	(485–839)	Closed
19–21 Aug 1982	13	749	(485–1,014)	Closed
11–12 Aug 1983	12	2,646	(2,094–3,197)	Closed
29–30 Aug 1984	13	308	(176–463)	Closed
12–15 Aug 1985	12	617	(397–838)	Closed
28 Aug–1 Sep 1986[4]	13	2,315	(1,631–3,020)	Closed

[1] Biomass estimates and confidence intervals were calculated by the "area swept" technique of Alverson and Pereyra (1969), using the equations developed by Smith and Bakkala (1982).
[2] Catches calculated from commercial samples and total pandalid catch (Albers and Anderson 1985).
[3] Survey curtailed due to severe weather.
[4] A 3.2 mm mesh liner was used during this survey.

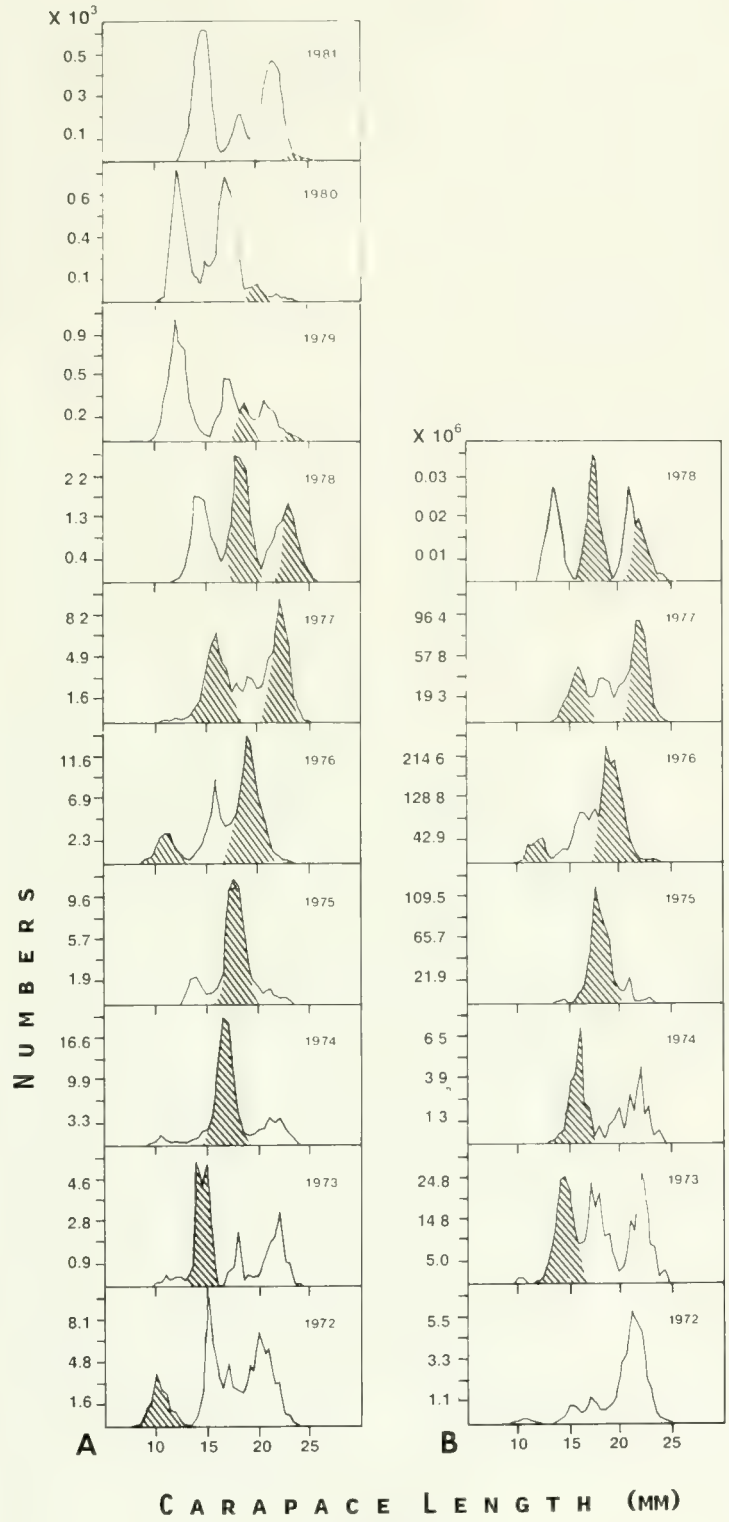


Figure 2

Size-frequency distributions of *Pandalus borealis* from Pavlof Bay, Alaska, in catch per kilometer from (A) annual research surveys, 1972–81, and (B) total numbers in the commercial catch, 1972–78. Dominant 1971 and 1975 size modes are shaded.

from each survey tow. Endopodite structure of the first two pleopods (Allen 1959) was used to separate the sexes. Length-frequency data by sex from commercial catch samples were provided courtesy of the ADF&G (211 Mission Rd., Kodiak, AK 99615).

Estimating mean size and abundance of year-classes

The total number of *P. borealis* in a survey or commercial catch was estimated for each 0.5 mm CL group as

$$\hat{N}_{ij} = n_{ij} \frac{C_j}{w_j} \qquad (1)$$

where

$\hat{N}_{ij}$ = number of *P. borealis* in the ith size interval taken in the jth haul (i = 1. . . . q; j = 1. . . . r),

n_{ij} = number of *P. borealis* in the ith size interval sampled from the jth haul,

C_j = weight of *P. borealis* in the jth haul, and

w_j = sampled weight in the jth haul.

Estimates of abundance for each size group were summed for all tows annually to form length-frequency distributions (Fig. 2). The technique of Macdonald and Pitcher (1979) was then used to separate and quantify year-class modes. Length was assumed to be normally distributed for a given year-class. The computer algorithm (Macdonald 1980) requires starting values of parameters (mean, standard deviation, proportion) for each component (year-class). Starting values for parameters were visually determined and the program iteratively computed maximum-likelihood parameters.

The estimated number of shrimp of a given year-class ($\hat{N}_k$) was calculated as

$$\hat{N}_k = \hat{P}_k \hat{N}.. \quad \hat{B} / \sum_{j=1}^{r} C_j, \qquad (3)$$

letting

$\hat{P}_k$ = estimated proportion of the kth year-class in the sample population N. . ,

$\hat{N}..$ = estimated total number of shrimp captured in a survey period, and

$$\hat{B} = \frac{A}{r} \sum_{j=1}^{r} [C_j/a_j]\, q, \quad (3)$$

where $\hat{B}$ = estimated biomass of *P. borealis*,
A = total survey area (Pavlof Bay >55 m; 302 km^2),
a_j = area covered in tow j, and
q = catchability coefficient of the sampling gear.

In the absence of better information, the catchability coefficient (q) in this analysis was set at 1.0. Strictly speaking, this only applies to shrimp sizes that are fully recruited to the sampling area and gear. Equation (3) is modified from Alverson and Pereyra (1969). Biomass estimates are conservative because small (<18 mm CL) shrimp are not fully vulnerable to capture.

Finally, the number of *P. borealis* of a given year class ($\hat{R}_k$) caught by the fishery between research sampling surveys was estimated as

$$\hat{R}_k = \hat{P}_k\, N..\, [L/W], \quad (4)$$

where $\hat{P}_k$ is calculated similarly to survey catches above,
$N..$ = total number of shrimp sampled from the commercial catch in a given year,
L = total landed weight of *P. borealis* between surveys, and
W = total sample weight from which $N..$ was calculated.

Determination of growth and mortality

Growth rates were estimated by following the 1971 and 1975 year-classes through a time series of length-frequency distributions (Fig. 2). The dominance of these year-classes minimizes the effect of overlap with adjacent modes. Nonlinear least-squares regression (Program BCG2, Abramson 1971) was used to fit von Bertalanffy growth curves to average size-at-age data.

Annual instantaneous total mortality rates (Z) for the dominant year-classes were calculated as

$$Z_k = -\ln (N_{k,t+1} / N_{k,t}) \quad (5)$$

where t = one year and $N_{k,t}$ and $N_{k,t+1}$ represent the relative abundance of the kth year-class in two consecutive years.

Estimated fishing (F) mortality was derived from estimated total mortality using Ricker's (1975) formula

$$F_k = \hat{\mu}\, Z_k / (1 - e^{-Z_k}) \quad (6)$$

where $\hat{\mu}$ = annual exploitation, the ratio of estimated catch in numbers (R_k from eq. 4) and estimated abundance (N_k from eq. 2) of the 1971 and 1975 year-classes.

Natural mortality (M) was calculated by subtraction:

$$M_k = Z_k - F_k. \quad (7)$$

Results and discussion

Estimates of age, growth, and mortality rates in this study were made for two dominant year-classes that could be followed through most of their life span. Assumptions underlying the estimates were that size modes represented year-classes, and immigration and emigration of Pavlof Bay shrimp were minimal.

Identification of year-classes

The 1971 and 1975 year-class modes were identified and followed through 1981 in length-frequency plots (Fig. 2, Table 2). The size at which dominant modes are first identified is between 10 and 11 mm CL. *Pandalus borealis* of this size are approximately 1.4 years old if it is assumed that larvae hatch in April, and early growth is similar to that reported by other investigators (Butler 1964, Ivanov 1970, Fox 1972, Skúladóttir 1981). The plots indicate similar patterns between the two year-classes, as well as close agreement in location of dominant modes in both the survey and commercial data (Fig. 2 and Table 2). Close agreement in the modal structure of the two independent data sets supported the assumption that the survey and commercial catch data were drawn from the same population and made estimation of fishing mortality possible. Commercial gear used comparable mesh and had a similar fishing configuration to our survey gear, except for the codend liner. The presence of a codend liner in survey sampling gear may explain the better definition of 1.4 year-old modes in survey samples due to the smaller effective mesh size.

Problems in identifying the age of the smallest modal group have been noted by other researchers (Fréchette and Parsons 1983). Entering year-class modes from survey data were assigned the age of 1.4. A smaller mode (mean of 6.5–7.5 mm CL; numbers not large enough to be depicted in Fig. 2) was designated age 0.4 (~146 days assuming an April hatch). Nunes (1984) reported that laboratory-reared *P. borealis* postlarvae reached 3.6–3.9 mm CL by about 110 days after hatch-

Table 2

Mean carapace length (CL), standard deviation (SD), and estimated number in survey area or estimated number caught in millions (N) of domination year-class components separated by the Macdonald and Pitcher (1979) method from Pavlof Bay, Alaska, trawl survey and commercial catch length-frequency samples.

	1971 year-class						1975 year-class					
	Survey			Commercial catch			Survey			Commercial catch		
	CL	SD	$N\times10^6$	CL	SD	$N\times10^6$	CL	SD	$N\times10^6$	CL	SD	$N\times10^6$
1972	10.06	0.79	388.48	10.24	0.75	0.78						
1973	14.28	0.55	561.33	14.16	0.79	98.30						
1974	16.47	0.73	2337.62	15.54	0.70	21.93						
1975	17.44	0.71	1252.43	17.65	0.72	450.55						
1976	18.96	0.87	1738.33	19.10	0.91	642.08	10.66	0.81	413.90	11.01	0.49	53.33
1977	21.75	0.99	1007.98	21.67	0.85	184.36	15.68	0.93	225.03	14.74	0.68	26.70
1978	22.98	0.84	177.96	22.17	0.48	21.56	18.20	0.90	317.99	17.17	0.56	71.44
1979	23.61	0.67	3.93				19.23	0.79	23.63			
1980							21.45	0.60	9.83			
1981							23.01	1.17	3.48			

ing. Seasonal trawl sampling and larval surveys at Chiniak Bay, Alaska, showed juvenile young-of-the-year reaching an average size of 7 mm CL by September (~153 days after hatching) for three consecutive years (E. Munk, Kodiak Lab., Alaska Fish. Sci. Cent., pers. commun., 10 June 1987). Since no other modes were found between this juvenile group and the larger-age 1.4 mode in survey sampling, it was assumed the age designation of these groups was correct. Skúladóttir (1981) found difficulty in assigning ages to entering size modes (average size 10–12 mm CL), probably because the stretched mesh gradually increased from 32 to 38 mm over five years of sampling (Hallgrímsson and Skúladóttir 1981). Fréchette and LaBonté (1981) also noted a similar problem with a mesh size of 38 mm. The mesh size in this study was 32 mm with a 32 mm codend liner, which may have helped in the retention of young shrimp.

Table 3

Average number of *P. borealis* caught per survey tow 1972–86. Tow length standardized to one nautical mile (1.85 km).

Survey	Number	Survey	Number
1972	160,752	1980	11,521
1973	61,410	1981	10,370
1974	208,356	1982	2,780
1975	126,322	1983	11,679
1976	199,566	1984	1,209
1977	160,074	1985	3,524
1978	49,879	1986	11,488
1979	16,066		

Abundance and variability of year-classes

The estimated biomass of *P. borealis* in Pavlof Bay peaked in 1977 and declined substantially in later years (Table 1). In response to reduced biomass, the fishery was closed by the ADF&G in 1979; the population subsequently stabilized at a lower level after 1978. The decline in abundance of the 1971 year-class (Table 2) reflected that of the total population (Table 1). The average number of *P. borealis* caught per survey tow declined steadily from approximately 199,000 in 1976 to 10,000 in 1981 (Table 3).

Dominant year-classes persisting in the population result from favorable conditions during their embryonic, larval, or juvenile stages. The relationship of shrimp landings to water temperatures prevailing during the spawning period 2 years earlier has been demonstrated in Gulf of Maine stocks (Dow 1966). Eggs incubated at 3 and 6°C resulted in larger newly hatched *P. borealis* larvae (1.41–1.49 mm CL) than those incubated at 9°C (1.09 mm CL) (Nunes 1984). If larger newly hatched larvae have a survival advantage, then colder incubation temperatures (6°C or lower) might enhance year-class strength. Warm temperatures may lead to lower survival of eggs and larvae of *P. borealis* due to increased egg parasitism and reduced food conversion efficiency (Paul and Nunes 1983). Minimum seawater temperatures in the study area normally range from 3 to 6°C (McLain et al 1979). Royer (1989) examined temperatures across the Gulf of Alaska and found very low-frequency fluctuations of ±2.0°C occur in the upper 250 m of the water column north of 55°N in the Gulf of Alaska (including Pavlof Bay). A cold temperature anomaly of more than 1.2°C was reported for the 1971–78 period in this region. These

anomalous low temperatures may have played a part in the formation of the strong 1971 and 1975 year-classes. Conversely, the relatively warm temperatures since 1980, perhaps peaking in 1984 (Royer 1989), may explain the lack of large year-classes in later years (Figs. 2, 3). It is possible that surveys of larval or juvenile abundance and related environmental parameters, mainly temperature, could be used to forecast future abundance trends.

Extreme variability in year-class strength can mean the success or failure of the commercial fishery. The 1971 year-class was dominant in commercial catches in Pavlof Bay during at least five fishing seasons (Fig. 2B). To calculate the contribution of dominant year-classes to the commercial catch, an average total weight, calculated from Pavlof Bay *P. borealis* length-weight data, $W = 0.00104\ CL^{2.70160}$ (Anderson 1981) was multiplied by the estimated number caught in each year-class (Table 2). During the years 1974–78, the 1971 year-class contributed about 70% and the 1975 year-class about 3% of the 12,384 metric tons of *P. borealis* harvested from Pavlof Bay. Although the commercial fishery was closed in Pavlof Bay from 1979 to 1986, little or no improvement in stock condition occurred. In Pavlof Bay, it appears that the *P. borealis* fishery was largely supported by a single year-class.

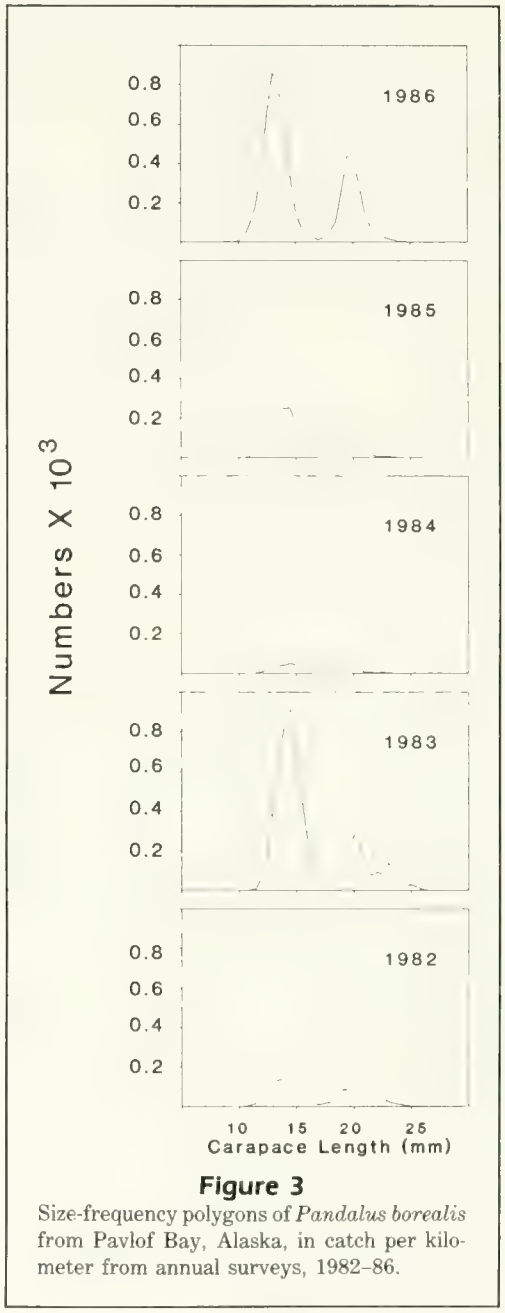


Figure 3
Size-frequency polygons of *Pandalus borealis* from Pavlof Bay, Alaska, in catch per kilometer from annual surveys, 1982–86.

Estimates of growth

Estimates of growth parameters in this study were generated only from the two dominant year-classes that could be followed through a time series (Fig. 2). Growth estimates depend heavily on the occurrence and definition of modes. *Pandalus borealis* have a synchronous and relatively abbreviated hatching period which gives rise to fairly well-defined size modes shortly after settlement of juveniles (Fréchette and Parsons 1983). Survey sampling was conducted in August–September, toward the end of the period of rapid summer growth. Studies that have continuously sampled throughout the spring and summer show growth slows in late summer, possibly as the result of spawning. Some instar growth is possible, however, even during mating and spawning, for the more frequently molting young males. I interpret the double-spike top of the 1971 year-class depicted in the 1973 survey data (Fig. 2A) as possibly representing year-class instar growth. As the shrimps age and transform to females, molting is reduced to perhaps two times a year, into and out of breeding dress (Allen 1959). Mode definition for year-classes after they become female is therefore not beset with an interpretation problem resulting from instar growth. The additional problem of overlap with adjacent but minor modes, especially with slower-growing females, is not so acute when using only dominant year-classes for growth estimates.

Separate von Bertalanffy growth curves were fit to average size-at-age data for the two dominant year-classes (Fig. 4). Parameters of the fitted relationship were $L_\infty = 29.64$, $K = 0.16$, and $t_0 = -1.30$ for the 1971 year-class, and $L_\infty = 26.31$, $K = 0.29$, and $t_0 = -0.47$ for the 1975 year-class. A Friedman two-way analysis of variance by ranks (Connover 1971) showed that members of the 1975 year-class were significantly ($P<0.001$) larger for a given age, indi-

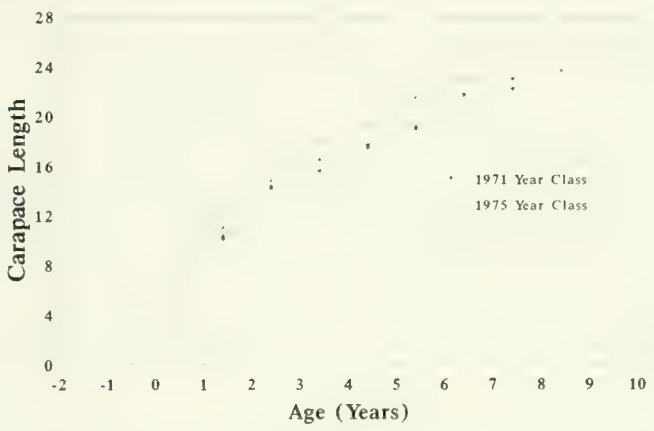


Figure 4

Von Bertalanffy growth curves generated from 1971 and 1975 year-class *Pandalus borealis* mean size-at-age data from both survey and commercial catch data.

Table 4

Mean size (CL) and standard deviation (SD) of 1.4 year-old *P. borealis* from 1972–86 survey samples in Pavlof Bay, Alaska.

Survey year	CL	SD
1972	10.06	0.79
1973	11.39	0.92
1974	10.62	0.92
1975	10.99	0.67
1976	11.84	1.98
1977	11.52	0.94
1978	11.72	0.70
1979	11.75	0.70
1980	13.21	0.83
1981	14.41	0.74
1982	13.70	1.12
1983	14.31	0.99
1984	13.97	1.24
1985	13.45	1.09
1986	13.24	1.04

cating a higher growth rate for this year-class. For example, the 1971 year-class attained average sizes of 16.47 and 21.75 mm CL at ages 3.4 and 6.4, respectively, whereas the 1975 year-class averaged 18.20 and 23.01 mm CL at these ages. Skúladóttir (1981) also detected large differences in growth rates between year-classes. In her study, one slow-growing year-class had a $K = 0.15$ and $L_\infty = 28$ which is similar to the parameters calculated for the 1971 year-class in this study. On the other hand, parameters calculated for the average of five fast-growing year-classes in her study indicated a $K = 0.23$ which is lower than the K (0.29) calculated for the 1975 year-class in the present study.

While growth of *P. borealis* is probably not related to overall population density, there is evidence of an inverse relationship relative to within year-class strength. Both the 1971 and 1975 year-classes hatched during periods of high overall population levels (Table 1), but the faster early growth of the 1975 year-class may be explained by its relatively lower abundance (Table 2) and, presumably, reduced competition for food during the juvenile phase. *Pandalus borealis* is an aggregating species exhibiting differential distribution by size, sex, age, and season (Shumway et al. 1985). Although most larvae are captured between 20 and 30 m in the water column (Haynes 1983), Wolotira et al. (1984) report a downward shift in vertical distribution with progressive stages of larval development. They theorized distribution differences reflect either a change in diet or distribution of food items. Berkeley (1930) also describes the apparent segregation of juveniles from the adult population. The effect of ecological separation of life-history stages could, therefore, explain differing growth rates among year-classes even though overall population density was high.

Since 1979, the occurrence of small shrimp (<12 mm CL) in survey samples has been much less than in previous years (Figs. 2A, 3). Three possible explanations for the virtual disappearance of this size-class are (1) small shrimp may only be retained when overall catch rates are as high as they were in 1972–77, (2) juvenile shrimp may not normally be found within the same area as larger adult shrimp except when high population levels force them into the less-preferred adult habitat, and (3) faster growth of juvenile shrimp may have led to entering year-classes growing beyond 10 mm CL to 13–15 mm CL since 1979. I believe the most plausible explanation for the disappearance of small shrimp from survey samples is faster growth of juveniles. Results of this study suggest growth is inversely related to year-class strength. The overall population decline of *P. borealis* in Pavlof Bay (Table 1) is attributed to the dying out of the relatively strong 1971 and 1975 year-classes and a series of relatively weak entering year-classes since 1979 (Figs. 2, 3). The 1.4 year-old group is now between 13.2 and 14.4 mm CL rather than the 10–11.8 mm CL that was observed for 1972–79 survey samples (Table 4). The possibility of missing size modes in this recent data series is low because sample sizes remained large (about 5000 shrimp per survey). Independent sampling of shrimp length frequency from cod stomachs captured in 1980 and 1981 trawl surveys showed cod consume smaller shrimp, probably the 0.4 year-olds (6.5 mm CL), than were found in trawl samples (Albers and Anderson 1985). Beyond 10 mm

CL, length frequencies were similar for both cod and trawl data, suggesting that the age designation of this larger 1.4 mode is correct.

Variability in growth rates of year-classes also causes variability in the age of full recruitment in survey sampling, owing to the size selectivity of our 32 mm mesh trawl. Recruitment was complete at ages 5.4 and 3.4 (18.96 and 18.20 mm CL) for the 1971 and 1975 year-classes, respectively. Likewise, selectivity experiments by Blott et al. (1983) showed complete vulnerability of 19 mm CL *P. borealis* in a 32 mm stretch mesh trawl. Fox (1972) reported full recruitment at age 3 (≈18.0 mm CL) in stocks of *P. borealis* from Kodiak Island, Alaska, in which sampling was accomplished with trawls having a mesh size similar to those in the present study.

Table 5

Annual exploitation (μ), total (Z), fishing (F), and natural (M) mortality rates for the 1971 and 1975 year-classes.

	1971 year-class				1975 year-class[2]			
Age[1]	μ	Z	F	M	μ	Z	F	M
3.4/4.4					0.225	2.600	0.632	1.968
4.4/5.4					0.000	0.877	0.000	0.877
5.4/6.4	0.369	0.545	0.478	0.067	0.000	1.038	0.000	1.038
6.4/7.4	0.183	1.734	0.385	1.349				
7.4/8.4	0.121	3.813	0.472	3.341				

[1] Ages of year-classes correspond with years 1974–79 for 1971 and 1978–81 for 1975 (see Table 2).
[2] Fishery closed in 1979; thus, μ and F are both zero.

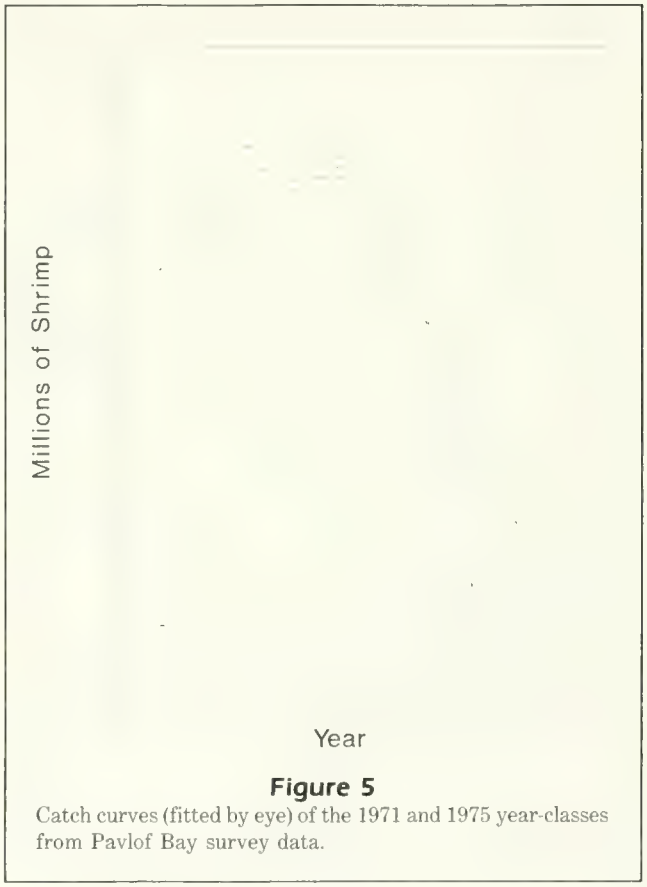


Figure 5

Catch curves (fitted by eye) of the 1971 and 1975 year-classes from Pavlof Bay survey data.

Mortality estimates

Total mortality estimates were based on year-class abundance after full recruitment to survey sampling (eq. 5; Table 5). The age of full recruitment to survey sampling was identified as 5.4 for the 1971 year-class and 3.4 for the 1975 year-class based on the visual inspection of the catch curve (Fig. 5). Since the commercial fishery was closed before the 1979 survey, total mortality rates estimated for the 1975 year-class beyond age 4.4 are equivalent to natural mortality. Table 5 also presents annual exploitation and fishing mortality rates estimated for both year-classes (from eq. 6). The 1971 year-class showed increasing natural mortality between ages 5.4 and 8.4, while fishing mortality remained relatively stable during this period.

Increasing total mortality with age for the 1971 year-class is attributed to increasing natural mortality since fishing mortality was constant. Apparent increases in natural mortality could also be caused by emigration of older individuals from the Pavlof Bay population, but this seems unlikely since it has been demonstrated that larger (older) shrimp are less active in diel vertical migration (Barr 1970) and would tend to be retained by the shallow entrance of Pavlof Bay. The observed higher natural mortality in this study may be the result of spawning stress or senescence since the 1971 year-class may have approached their maximum longevity. Predation by Pacific cod *Gadus macrocephalus* may have also contributed to the high mortality observed from ages 6.4 to 8.4 when cod catches increased from 10 to about 500 kg per nautical mile towed (Albers and Anderson 1985).

The 1975 year-class showed its highest calculated natural mortality between ages 3.4 and 4.4 (Table 5); however, these rates were subsequently lower. After closure of the fishery, the total mortality rates for the 1975 year-class beyond age 4.4 are equivalent to natural mortality. Albers and Anderson (1985) reported the significance of Pacific cod predation on *P. borealis* in Pavlof Bay. Pacific cod abundance peaked in 1979

and declined to about one-sixth of its former abundance by 1981. Lower observed natural mortality for the 1975 year-class beyond age 4.4 could be explained by decreasing cod predation.

Mortality estimates rely not only on the suitable definition of the year-class modes but also on the accuracy of biomass estimates (see eq. 2). Accuracy of biomass estimation is a function of the vulnerability, gear selectivity, and accessibility of shrimp in Pavlof Bay to the annual surveys. Knowledge of the life history of *P. borealis* were used to address these sources of variability in survey sampling. The late summer-fall period was chosen for sampling because *P. borealis* may be more vulnerable to capture due to the formation of mating and spawning aggregations. Small males and the larger females are not segregated, and even juvenile shrimp ≈6mm CL can be found in these aggregations. Sampling was restricted to daylight hours to minimize the effect of diel vertical migration; thus, shrimp were more susceptible to capture by bottom trawling. Shrimp smaller than 18mm CL are known to be less vulnerable to capture with the 32mm mesh survey sampling gear. Sampling with smaller mesh (3.2mm) in 1986 did indicate that more small shrimp could be captured, but small mesh sampling of the entire population was not deemed feasible due to increased sorting time.

Biomass estimates are considered conservative due to the lesser vulnerability of small shrimp. Likewise, larger/older shrimp may be able to escape capture by swimming out of the water column sampled by the survey trawl, leading to an overestimate of mortality. The high opening shrimp trawl used in this study (Wathne 1977) was designed to sample a substantial portion (3.8–4.4m off bottom) of the water column. Biomass trends tend to refute avoidance of larger shrimp as a source of error.

Biomass estimates, while they may not be an absolute estimate of the population size, can represent an index. Sources of variability that could affect the validity of biomass estimates being used as an index were controlled. Survey timing, gear, methods, and even vessel type were the same throughout the survey series. Survey sampling methodology, while minimizing, may not always eliminate possible changes caused by availability of shrimp. *Pandalus borealis* may be more vulnerable to capture during mating and spawning because dense aggregations are probably beneficial for mating success. The exact timing of this event may vary from year to year. As an example, the 1972 and 1974 surveys both took place during the second week in September (Table 1). In 1972, about 60% of females were carrying eggs externally while only head roe (egg mass clearly visible under carapace) females were found in 1974. Changes in availability probably explain the dip in the catch curve for the 1971 year-class at age 4.4 and at 2.4 for the 1975 year-class (Fig. 5). These apparent changes in availability perhaps associated with some life-history stage or abiotic factor should be studied in order to improve both biomass and mortality estimates.

Table 6

Percent female of the 1971 and 1975 year-classes at age (years) from Pavlof Bay, Alaska, survey sample analysis.

	Age							
Year-class	1.4	2.4	3.4	4.4	5.4	6.4	7.4	8.4
1971	0	0	0	2	38	100	100	100
1975	0	0	0	100	100	100	—	—

Sex transformation

The rate of transformation from male to female was considerably different for the two dominant year-classes studied (Table 6). Some members of the 1971 year class initiated sex transformation during their fourth year; however, others transformed during either their fifth or sixth year. In contrast, all members of the 1975 year-class initiated and completed transformation during their fourth year. The age at and rate of sex change for a year-class also appear to be closely related to year-class size or overall population density. Charnov (1979, 1981) proposed a model in which high mortality rates lead to a shorter male phase. Charnov et al. (1978) also considered how natural selection might act to alter the sex ratio of Pandalid shrimp in response to environmental influences. I feel that accelerated sex transition observed for the 1975 year-class in this study was influenced by short-term phenomena and is evidence of the labile timing in sex change of this species. The occurrence in 1980 and again in 1984–86 of the smallest ovigerous females ever sampled (13.0mm CL) is further evidence that accelerated sex reversal may be a possible mechanism by which northern shrimp attempt to increase reproductive capacity in the face of decreasing density (Table 1). Charnov and Anderson (1989) reported on an analysis of Pavlof Bay *P. borealis* that demonstrated the size of shrimp at the time of sex-transformation changes through time in relation to changes in the breeding size distribution.

Stock/recruit relationship and yield

While a compensatory relationship between lower population levels or density and the occurrence of early

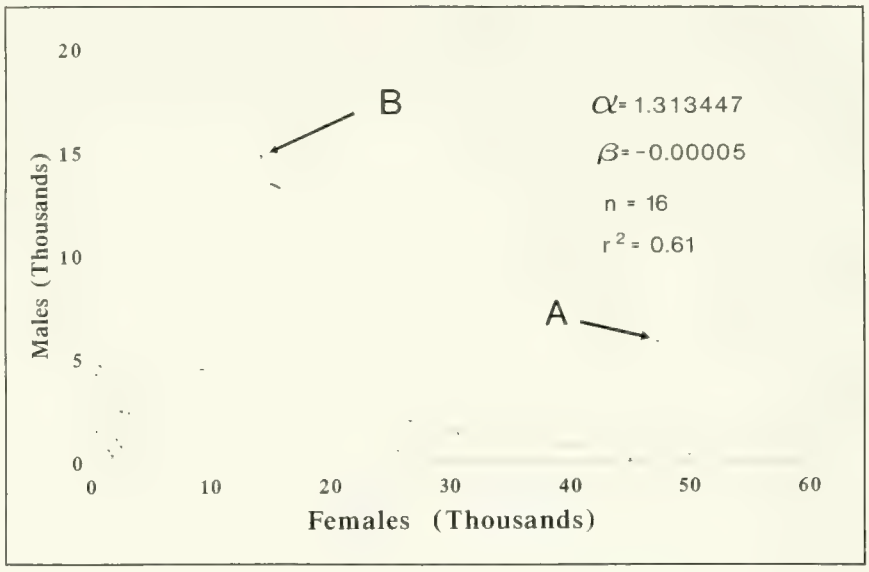


Figure 6
Spawner/recruit curve fit on female *Pandalus borealis* caught per kilometer as index of spawning biomass, and 1.4 year-olds (lagged one year) as recruit index, captured in Pavlof Bay shrimp surveys 1972–86. Points labeled A and B show effect of strong 1.4-age male year-classes of 1973 and 1975, respectively.

transformation of shrimp has been suggested in this study, the relationship between stock and recruitment appears to elude suitable definition. Using the average catch of females per tow as an index of spawning population and the catch rate of 1.4 year-old males as an index of recruits (lagged one year), a Ricker (1975) stock-to-recruit relationship was constructed (Fig. 6). While other combinations representing spawning and recruit biomass were tried, this combination gave the best fit to the recruitment function. Possible reasons for this combination rendering the best fit are that females are almost fully vulnerable to trawl capture and remain near the bottom during the fall survey period. On the other hand, while the 1.4 year-old males are not fully vulnerable to trawl capture, they do seem to represent a good relative index of incoming year-class strength. When dominant year-classes could be identified and followed through time, they were first identified as being relatively strong as 1.4 year-olds (Fig. 2). Since the 1.4 year-old mode is usually well separated from the remaining frequency distribution, weak as well as strong incoming year-classes could be quantified with the mode-separation technique.

Extreme fluctuations in the abundance of young year-classes make it difficult to devise management strategies. In some years, a relatively small spawning stock may give rise to a large year-class. The fit to the stock recruitment curve (Fig. 6) shows that the majority of the data points mostly conform to the fitted relationship. Outlying points labeled as A and B (A, 1973 year-class males (age 1.4) vs. brood females of 1972; and B, 1975 year-class males (age 1.4) vs. brood females of 1974) illustrate how relatively dominant 1.4 year-old male year-classes can push data points well outside the bounds of the curve (Fig. 6). The relative abundance of 1.4 year-old shrimp is probably a function of the variable survival of larvae and juveniles in response to environmental conditions rather than spawning biomass. The inadequacy of the fitted stock to recruit function to describe these important contributions to stock biomass means that other methods for defining management are needed. Therefore, strategies based on yield-per-recruit of dominant year-classes were examined.

Figure 7
Biomass vector (in the absence of fishing) calculated using the technique of Paulik and Bayliff (1967) for the 1971 and 1975 year-classes.

Incorporating the growth and mortality estimates from this study into a Ricker yield model (Paulik and Bayliff 1967) indicated that maximum biomass, in the

absence of harvest, would be achieved at a relatively early age (Fig. 7) and small size. The maxima of biomass vectors were attained between age 2.4 (14.3 mm CL) and 3.4 (16.5 mm CL) for the 1971 year-class, and at age 3.4 (18.2 mm CL) for the 1975 year-class (Fig. 7). A management strategy based on maximizing the yield-per-recruit for the 1971 year-class would have resulted in the harvest of mostly male shrimp prior to their transformation to females. A similar finding was also reached by Abramson and Tomlinson (1972) in yield studies of *Pandalus jordani*. Harvesting more young shrimp may also lead to a possible lower economic return due to market resistance to small meats. Optimum management of Pandalid shrimp fisheries probably involves a trade-off between size-related economic return and larger yields from the harvest of young shrimp.

Conclusions

1 The bathymetric features of the Pavlof Bay region make it an ideal area for studying populations of *P. borealis*. The confining sills probably allow little immigration or emigration of shrimp. Thus dominant size modes, representing year-classes, could be followed through time in both the research survey and commercial data sets. It is necessary to rely on following dominant size modes to gain insight into population parameters owing to the problem of overlap with less dominant year-classes in the size-modal structure.

2 The Pavlof Bay population of *P. borealis* showed significant differences in year-class strength, with the 1971 year-class predominating during the study. Dominant year-classes are first detected when they are young (1.4 years old). Biotic or abiotic factors that control year-class strength have their greatest effect during the larval and juvenile stages.

3 There is evidence that growth may be inversely related to year-class strength. Since 1979, 1.4 year-old shrimp have averaged 13–15 mm CL rather than the 10–11 mm CL observed prior to 1979.

4 Age at sex transition was highly variable for the two dominant year-classes studied. The 1971 year-class showed transition over three years, while the 1975 year-class completed transformation in one year.

5 Total mortality rates of Pavlof Bay *P. borealis* are some of the highest reported for the species (Fréchette and Parsons 1983, Teigsmark 1983, Hopkins and Nilssen 1990) and are mostly a reflection of the high natural mortality rates. High natural mortality rates for the 1971 year-class are attributed to intense predation by Pacific cod (Albers and Anderson 1985). After the cod population subsided within the Bay, natural mortality, along with total mortality, declined.

6 Yield could have been maximized by harvesting more young (male) shrimp, since mortality rates were high for the year-classes studied.

Worldwide, other *P. borealis* fisheries have experienced similar cycles of high and low abundance (Balsiger 1981) that characterized the rise and fall of western Gulf of Alaska fisheries in the 1970s. The decline of shrimp in Pavlof Bay was probably inevitable, regardless of the presence of a fishery, since many adjacent areas lightly or seldom fished experienced similar population declines (Anderson and Gaffney 1977). These declines may be directly attributable to the demise of a single or series of strong year-classes. Little is known about the parameters controlling shrimp natality and its relationship to subsequent recruitment. This problem deserves study, along with the effects of predation (Albers and Anderson 1985) and ecological and environmental parameters (Nunes 1984). Continuing shrimp research surveys in Pavlof Bay may lead to understanding the dynamics and perhaps the mechanisms driving the cycle of low and high shrimp abundance in the western Gulf of Alaska.

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Abstract.–Changes in total body energy content of adult (total length ~9 cm, wet mass ~9 g) northern anchovy *Engraulis mordax* were estimated by sampling captive groups swimming at 8.7 and 21.1 cm/s for 12 hours daily. Anchovy were fed euphausiids at rations of 5 and 3.4% of fish wet mass per day (~54 and 37 cal · g fish wet mass^{-1} · day^{-1}, respectively). Gross energy conversion efficiency increased with ration levels and declined with swimming speed, ranging from 39% to 1%. Dry mass and lipid losses were estimated in fasting fish swimming at the same speeds. Energy losses were 17.6 and 28.2 cal · g fish wet mass^{-1} · day^{-1} at the slow and fast speeds, respectively. The proportion of food energy used for growth and maintenance metabolism was about 65%. A model derived for adult anchovy metabolism was consistent with observed growth and reproduction rates, and the few measurements of ration and swimming speed in nature.

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Bioenergetics and Growth of Northern Anchovy *Engraulis mordax*

Christofer H. Boggs

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole Street, Honolulu, Hawaii 96822-2396

The incorporation of energy from food into growth and reproduction by northern anchovy *Engraulis mordax* has been roughly quantified. Prey abundance influences the rate of anchovy reproduction during subsequent years, according to time-series analysis (Smith and Eppley 1982). Abundant food probably results in more energy intake and storage. Energy available for growth and reproduction by northern anchovy in the wild has been estimated at 12.8% of energy intake, based on laboratory measurements of gross energy-conversion efficiency (Hunter and Leong 1981). At 12.8% efficiency, the daily ration needed for average growth and reproduction was estimated to be 4-5% of fish wet mass (Hunter and Leong 1981), which is towards the high end of the range of field estimates for engraulids (Blaxter and Hunter 1982). However, food intake and energy demands vary. An energy budget model could help explain and predict the effect of food availability on anchovy growth and reproduction.

Gross energy-conversion efficiency is the net energy remaining after food assimilation and metabolic losses divided by the total energy consumed as food. Thus, gross energy-conversion efficiency should tend to increase with ration and decrease with increased swimming activity. The impact of swimming activity on clupeoid metabolism has been described for Pacific sardine *Sardinops caerulea* (Lasker 1970), Atlantic menhaden *Brevoortia tyrannus* (Durbin et al. 1981), and Peruvian anchoveta *E. ringens* (Villavicencio 1981). Estimated metabolic rates of adult northern anchovy (S. Kaupp, R. Lasker, and R. Leong, a table of estimates obtained from J.R. Hunter, Southwest Fish. Sci. Cent., NMFS, NOAA, P.O. Box 271, La Jolla, CA 92037, unpubl. data) are about twice as high as those of its congener, *E. ringens*, at swimming speeds of about 1 body length/s. This difference is not small in relation to the overall energy budget of engraulids; therefore, better estimates of swimming metabolism are needed. The present study measures the energy expended for metabolism by northern anchovy at different swimming speeds, examines the effect of ration and metabolic rate on gross energy-conversion efficiency, and derives a model for adult anchovy metabolism.

Methods

The flume

Juvenile and adult northern anchovy ranging from 2 to 7 g wet mass were purchased from live-bait dealers in February 1984 and acclimated to laboratory conditions for 2–4 months prior to being transferred to an open flume for exercising the fish. Procedures for keeping live anchovy are described in Leong (1971) and Hunter and Leong (1981). Fish were fed 0.09 g Biomet trout pellets per fish per day until the study began.

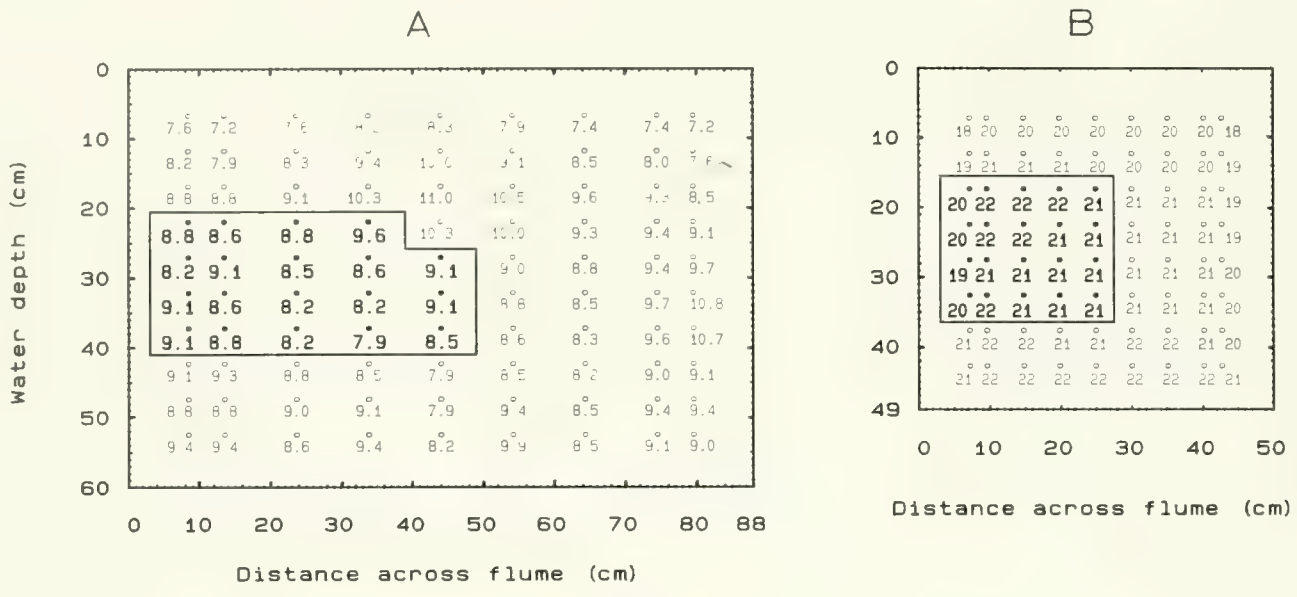

Figure 1

Cross-sections of two flume sections showing water speed (in cm/s). Outlined areas were habitually occupied by the fish, and the enclosed speed values (shown in bold) were averaged to obtain the swimming speed in the (A) slow and (B) fast sections.

The open flume was composed of two connected sections, the second section narrower and shallower than the first, resulting in a more rapid flow. The first section (the slow section) measured 244×88×60 cm (1290 L), and the second (the fast section) measured 244×50×49 cm (600 L). A 20 hp pump at the downstream end of the flume recirculated about 50 L/s of seawater through a feed pipe back to the upstream end of the flume. Water flowed through a tapered expansion section packed with gratings to even the flow. The whole flume was inside a 15,000 L tank. Fresh filtered seawater was added to the recirculating water in the flume at a rate of 20–30 L/minute. Temperature was maintained at 16.5–17.5°C.

Cross-sectional current profiles in each section were measured with a Marinco B-10 ducted impeller current meter. Baffles upstream from each section were adjusted to make the current profiles as uniform as possible, and gratings at the ends of each section confined the fish. Anchovy acclimated to the flume occupied habitual areas within the two sections (Fig. 1). The current measurements in these areas were averaged to estimate swimming speed. The pump was operated 12 hours daily during "daylight"; the photoperiod was 13L:10D with half-hour "dawn" and "dusk" periods.

Fish were anesthetized with quinaldine prior to transfer to the flume. During transfer, the fish were sorted and selected by size. A greater number were put in the larger (slow) flume section to make fish density similar in both sections. Initially 1600 and 1000 fish were put into the slow and fast sections, respectively. The 12-hour swimming regime was built up over 8–10 days and then maintained for 2–3 weeks for each treatment.

Treatments

Three levels of energy intake—high, zero, and low rations (in that order)—were imposed at two swimming speeds, making a total of six treatment combinations (Table 1). At each ration level, slow- and fast-speed treatments were applied concurrently in the two flume sections. The initial stock of fish was enough for the high- and zero-ration treatments. The flume was restocked for the low-ration treatments, but the number of laboratory-acclimated fish available was low (Table 1).

Starting 8–10 days before the treatments began, food type was changed to commercially obtained frozen euphausiids (species not identified). Anchovy were fed thawed euphausiids for 1 hour (high ration) or 0.5 hour (low ration) during the end of the daily swimming period. Food placed in 15 L containers of water above the flume flowed into perforated tubes (2.5 cm diameter, 0.6 cm perforations) stretched across the front of the two sections. Screens were temporarily inserted

Table 1

Summary of feeding levels in sequence of application, 12-hour enforced speeds, average fish mass, and estimated daily rations for the six treatments using the northern anchovy *Engraulis mordax*. N_C = initial number of fish in each flume section at the start of each treatment, N = total number killed for samples (number of samples in parentheses), and D = percentage of fish that died.

Treatments						Fish mass (g)			
Feeding level	Speed (cm/s)	N_C	N	D (%)	Wet mass of food per fish* (g/day)	Wet	Dry	Corrected daily ration** (% wet mass)	Ration energy (cal·g fish wet mass^{-1}·day^{-1})
High	8.7	1392	331 (4)	39	0.443	9.02	2.40	5.06	55.7
	21.1	674	184 (4)	49	0.442	9.83	2.57	4.73	52.0
0	8.7	469	291 (5)	8	0	8.86	2.68	0	0
	21.1	131	86 (3)	27	0	9.32	2.96	0	0
Low	8.7	416	298 (4)	16	0.227	6.82	1.92	3.42	37.6
	21.1	177	111 (2)	37	0.285	8.67	2.66	3.38	37.2

*Average from daily amounts dispensed and equations in Figure 2.
**Corrected for gastric evacuation (cf. Equation 4 in text).

to prevent food in one section from passing to the other. Uneaten food collected on the screens was weighed.

Rations were chosen to match the high ration (4–5%) estimated by Hunter and Leong (1981), and a lower ration (3%) in the middle of the range of field estimates (Blaxter and Hunter 1982). The zero ration was included so that metabolism could be estimated from the loss of body energy.

Preliminary estimates of rations were made from the net mass of food dispensed and the number of fish in each treatment (Table 1). Preliminary ration estimates were calibrated based on the amount of food in stomachs after feeding, corrected for gastric evacuation. To estimate the gastric evacuation rate, 15–24 fish were killed and stomach contents weighed once per hour for 7 hours on the seventh day of the first treatment.

Removing and counting fish

A sample of fish (Table 2)* was collected in one sweep of a large dipnet at the beginning and end of each treatment, and every 4–7 days during five of the six treatments. In the low-ration, fast-speed treatment there were enough fish only for the initial and final samples. At least 20 fish were planned for each sample, but the number of fish netted was sometimes lower, or much higher (Table 2)* because the sample was taken quickly to avoid disturbing the fish.

The standard length of sampled fish, their wet mass, and the wet mass of stomach contents were measured.

*In the zero-ration treatments, sample size was the same as the number dried (Table 3).

A subset of about 20 fish from each sample and the combined stomach contents from 9 samples were dried for 6 days at 55°C, cooled in desiccators, and weighed.

A census was kept on the number of fish in each section of the flume based on rapid counts of the fish transferred to the flume, minus removals due to sampling and mortality. Dead fish were collected and measured each day. The initial counts were accurate to within 10% of the total number collected at the end of the treatments. A corrected census, figured from the total counts, was used in the final calculations.

Data analysis

Within each treatment, trends in sample means (i.e., length) or calculated values (i.e., kcal/fish) were expressed as slopes in relation to elapsed time by using linear regression (method of least squares). When only two samples were collected in a treatment, the difference over time was calculated. The significance of slopes, differences between initial and final sample means, and differences between values estimated from regression (i.e., log of dry mass) were evaluated with t-tests.

Apparent growth trends in some treatments were corrected to account for high mortality of fish smaller than the treatment mean. If there was no significant change in length (e.g., in zero-ration treatments), then no correction for mortality was made and length was assumed to be constant. An approximation of the bias in group mean length caused by mortality each day was calculated as the difference between the apparent mean length of the group each day (L_A) and the mean length calculated by including the dead fish collected that day,

Table 2

Increase in standard length (95% confidence intervals in parentheses) with time during the four feeding treatments and the correction for size-specific mortality. N_C = number of fish in each flume section before the first sample, N = sample size, N_S = stomach content sample size, and NA = not applicable.

Ration (cal·g^{-1}·day^{-1})	Speed (cm/s)	Day	N_C	N	N_S	Mean length (mm)	Apparent growth in length	Mortality bias (mm/day)	Actual growth in length
High	Slow								
55.7	8.7	0	1392	101	0	88.1 (±1.2)			
		7	1160	168	157*	90.1			
		14	773	29	29	95.4			
		21	556	33	33	91.0 (±2.5)	0.202 (±0.569)	0.155	0.047
High	Fast								
52.0	21.1	0	674	99	0	88.9 (±1.1)			
		7	489	33	33	91.8			
		14	327	22	22	95.4			
		21	187	30	30	94.1 (±2.5)	0.277 (±0.324)	0.244	0.033
Low	Slow								
37.6	8.7	0	416	75	24	84.4 (±1.1)			
		7	319	78	24	84.1			
		14	212	70	24	85.5			
		20	126	75	24	86.0 (±1.3)	0.092 (±0.099)	0.023	0.069
Low	Fast								
37.2	21.1	0	177	52	24	93.9 (±1.7)			
		16	59	59	24	92.9 (±1.7)	-0.063	NA	0

*Total of 8 samples (Fig. 3) collected 0–7 hours after feeding (N_S = 23, 21, 19, 16, 24, 15, 15, and 24, respectively).

$$\text{Daily bias} = L_A - \left| \frac{(L_A N_C) + (L_M N_M)}{N_C + N_M} \right| \text{ mm/day}, \quad (1)$$

where N_C was the number of fish in the treatment group at the end of each day, N_M was the number of dead fish that day, and L_M was the mean standard length of the dead fish that day. The L_A was calculated from a regression of sample mean lengths on elapsed time over the course of the treatment. The slope of this regression (L_A on elapsed time) was the apparent growth (Table 2), which was corrected by the average of the daily biases to estimate the actual increase in fish length.

Fish mass was estimated from corrected length using log–log regressions of dry mass on standard length for each sample. The regression estimate for each sample was calculated by assuming that length increased at the corrected rate for that treatment.

From each sample, a subset of four fish, chosen to best match the estimated length and dry mass of the sample, was analyzed for fat content by using Soxhlet extraction with chloroform-methanol (2:1). Fat content of food removed from stomachs was also measured. Total energy content of fish and food was estimated from published values (Brett and Groves 1979, Hunter and Leong 1981) for heat of combustion. The rate of energy loss or gain in each treatment was calculated as the regression slope of fish energy content in each sample versus elapsed time.

Results

Rations

Anchovy stomach contents from 12 samples (Table 2) were weighed immediately after feeding. The average amount of food in the stomachs was less than (but correlated with) the net amount of food that was dispensed per fish (Fig. 2). The difference was too large to be due to the rate of gastric evacuation. A portion of the food passed through gaps in the bottom of the flume sections and into the surrounding tank. Recirculation of this food was prevented by screens. Regressions of stomach contents on food dispensed (Fig. 2) suggested that a greater proportion of the food dispensed was eaten in the high-ration, fast-speed treatment than in the other treatments. Although the regressions were not significantly different, they were used to estimate stomach contents separately for each speed on days when stomach contents were not sampled. The average of the resulting daily estimates was calculated for each treatment (Table 1).

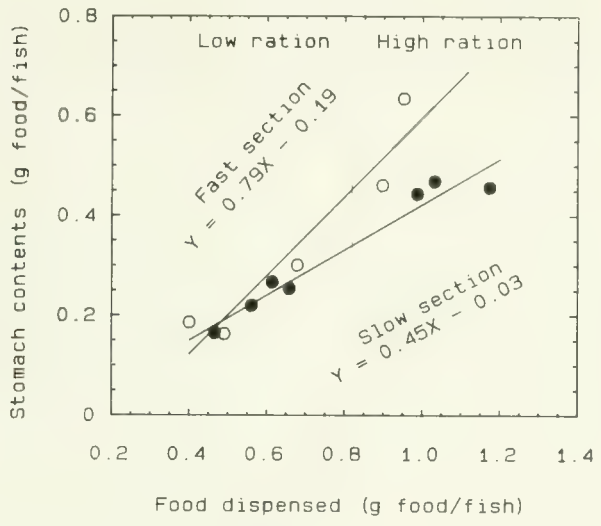

Figure 2

Relationship between the net amount of food dispensed per anchovy and stomach contents (wet mass of food/fish) after feeding in the slow (filled circles) and fast sections (open circles) of the flume. Each point is the mean for a sample of N_S fish (Table 2).

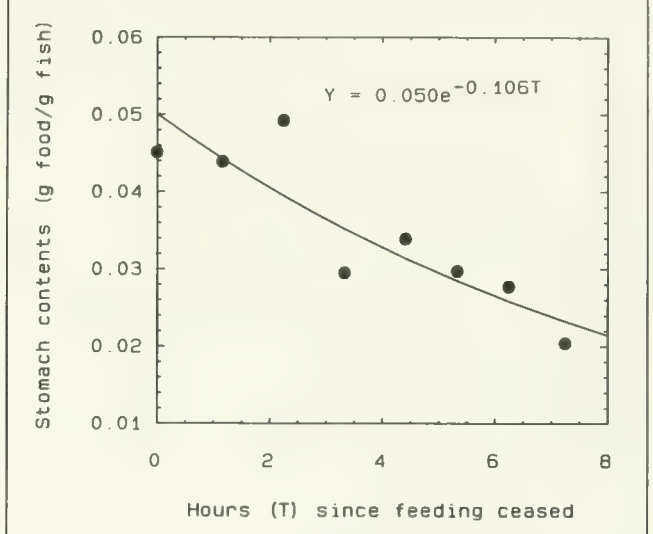

Figure 3

Gastric evacuation rates of northern anchovy fed euphausiids (food wet mass/g wet mass fish). Each point is the mean for a sample of N_S fish (Table 2).

Evacuation of the food from the stomach was slow (Fig. 3). The absence of an immediate decline in stomach contents after feeding suggested a gastric pause or coprophagy, although this result may be due to sampling errors. The following regression (using a semilog transformation) of mean stomach contents (Y in grams food/gram fish) versus elapsed time (T in hours after feeding stopped) describes the data from eight hourly samples (Table 2, Fig. 3):

$$\log_e Y = -2.995 - 0.106\ T \quad (N\ 8,\ r^2\ 0.81). \quad (2)$$

Taking the antilog

$$Y = 0.05\ e^{-0.106\ T}\ \text{g food / g fish}, \quad (3)$$

the actual amount of food consumed (C_T) between the initiation and cessation of feeding was estimated (Elliott and Persson 1978) as

$$C_T = \frac{[S_T - (S_0\ e^{-dT})]\ rT}{1 - e^{-dT}}\ \text{g food}, \quad (4)$$

where S_T was the amount of food found in stomachs at the cessation of feeding, and d = 0.106 (from Equation 3). No food was in the stomachs at the initiation of feeding (S_0 = 0). For 1 hour of feeding, C_T equaled 1.054 S_T, and for 0.5 hour of feeding, C_T equaled 1.027 S_T. Thus, only a slight correction of mean stomach content estimates was needed to calculate the rations (Table 1).

The water content of food (euphausiids) averaged 78.4% (*N* 9, SD 1.7%); therefore, dry mass averaged 21.6% of wet mass. The fat content of the food averaged 21.8% of dry mass (*N* 3, SD 3.6). S. Kaupp (NMFS Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92037, pers. commun., March 1984) found that the average protein content of euphausiids (species not identified) was 43.5% of dry mass (*N* 25, SD 0.20). The remaining dry mass (24.7%) was estimated to consist of ash and chitin in roughly equal amounts, since Lasker (1966) found that molts and ash each made up about 10% of dry mass in *Euphausia pacifica*. Assuming 9.2kcal/g for fat, 5.65kcal/g for protein, and 4.1 kcal/g for carbohydrate (Brett and Groves 1979), the total caloric content of the food was

$$\left[\frac{21.8}{100}\ 9.2\ \frac{\text{kcal}}{\text{g dry}}\right] + \left[\frac{43.5}{100}\ 5.65\ \frac{\text{kcal}}{\text{g dry}}\right] + \left[\frac{12.4}{100}\ 4.1\ \frac{\text{kcal}}{\text{g dry}}\right] = 5.09\ \frac{\text{kcal}}{\text{g dry food}}$$

and

$$5.09 \frac{\text{kcal}}{\text{g dry food}} \left| \frac{21.6\text{g dry}}{100\text{g wet food}} \right| = 1.1 \frac{\text{kcal}}{\text{g wet food}}.$$

Growth in length

Final mean length was significantly higher than the initial mean length in all feeding treatments except the low-ration, fast-speed treatment (t-test, $P \leq 0.05$; Table 2). However, the slopes of the regressions describing the apparent rates of growth (in length) were not significantly different from zero, because of the variation not explained by growth or selective mortality. The fish schooling in the flume may have sorted themselves by size so that the dipnet frequently caught a sample containing larger- or smaller-than-average fish. The coefficient of variation of length in each sample ranged from 5 to 7%. The low number of samples would make this an important source of error.

Table 3

Regressions of the natural log of dry mass ($\log_e$ Y) on the log of standard length ($\log_e$ X) estimated from actual growth (cf. Table 2), and measures of fat content (N 4) used to estimate dry mass, total energy, caloric growth, and energy loss during the six treatments. Estimates in brackets assume no increase in length; 95% confidence limits in parentheses. N = number of fish dried.

Treatment	Day	N	Regression equation	Length (mm)	Log of dry mass from regression	Dry mass (g)	Fat content (%)	Total energy (kcal)
High ration, slow speed								
	0	25	$\log_e Y = 3.861 \log_e X - 16.664$	89.04	0.668 (±0.091)	1.95	36.7	11.70
	7	32	$\log_e Y = 5.241 \log_e X - 22.814$	89.36	0.732	2.08	39.8	12.87
	14	19	$\log_e Y = 4.679 \log_e X - 20.333$	89.69	0.705	2.02	40.9	12.61
	21	23	$\log_e Y = 4.605 \log_e X - 19.784$	90.02	0.939 (±0.059)	2.56	43.9	16.30
				[89.04]	[0.888 (±0.059)]	[2.43]		
High ration, fast speed								
	0	24	$\log_e Y = 5.524 \log_e X - 23.943$	88.68	0.832 (±0.078)	2.30	41.7	14.39
	7	23	$\log_e Y = 3.893 \log_e X - 16.587$	88.91	0.883	2.42	43.7	15.38
	14	12	$\log_e Y = 5.193 \log_e X - 22.467$	89.14	0.851	2.34	43.8	14.89
	21	20	$\log_e Y = 4.574 \log_e X - 19.611$	89.37	0.939 (±0.056)	2.56	44.8	16.42
				[88.68]	[0.903 (±0.060)]	[2.47]		
Low ration, slow speed								
	0	24	$\log_e Y = 4.515 \log_e X - 19.493$	84.06	0.515 (±0.062)	1.67	38.4	10.16
	7	24	$\log_e Y = 4.839 \log_e X - 20.856$	84.54	0.616	1.85	41.1	11.51
	14	24	$\log_e Y = 5.485 \log_e X - 23.712$	85.02	0.657	1.93	39.2	11.83
	20	24	$\log_e Y = 5.539 \log_e X - 24.050$	85.44	0.586 (±0.066)	1.80	40.5	11.15
				[84.06]	[0.496 (±0.067)]	[1.64]		
Low ration, fast speed								
	0	41	$\log_e Y = 3.352 \log_e X - 14.245$	93.4	0.963 (±0.032)	2.62	46.4	17.02
	16	49	$\log_e Y = 3.906 \log_e X - 16.733$	[93.4]	[0.988 (±0.047)]	*[2.62]	46.8	17.07
No food, slow speed								
	0	19	$\log_e Y = 4.587 \log_e X - 19.767$	92.52	1.000 (±0.076)	2.72	46.2	17.38
	4	24	$\log_e Y = 4.975 \log_e X - 21.499$	do.	1.025	2.79	47.6	17.96
	8	23	$\log_e Y = 5.293 \log_e X - 23.041$	do.	0.923	2.52	44.2	15.76
	12	21	$\log_e Y = 4.838 \log_e X - 21.016$	do.	0.888	2.43	45.1	15.36
	16	24	$\log_e Y = 5.611 \log_e X - 24.716$	[92.52]	[0.914 (±0.063)]	[2.49]	43.1	15.56
No food, fast speed								
	0	21	$\log_e Y = 3.553 \log_e X - 14.947$	93.48	1.176 (±0.064)	3.24	45.2	20.97
	6	23	$\log_e Y = 4.903 \log_e X - 21.210$	do.	1.039	2.83	46.8	18.57
	12	42	$\log_e Y = 3.542 \log_e X - 15.066$	[93.48]	[1.007 (±0.051)]	[2.74]	46.1	17.82

* Assumed no change in dry mass since the difference was not significant.

Estimates of actual growth (in length), as corrected for mortality (Table 2), appeared similar to those for 1- to 2-year-old anchovy in nature based on otolith increments (Spratt 1975), but were lower than those measured by Hunter and Leong (1981) in the laboratory. No increase in length was indicated during the low-ration, fast-speed treatment, so no correction was made for mortality. The most rapid length increase (0.069 mm/day) was estimated for the group with the smallest mean size (Table 2). This group underwent the low-ration, slow-speed treatment yet appeared to have a faster rate of growth (in length) than did the high-ration, slow-speed group. This might suggest that the increase in length was size-dependent and somewhat independent of the net energy surplus.

Mortality was highest during the high-ration treatments and lowest in the low-ration and fasting treatments, especially at slow speed (Table 1). Fish bumped into the gratings between flume sections during feeding, which may have led to a high rate of injuries resulting in death. The size bias in mortality might have resulted from large fish being less often injured by the gratings. However, the treatment with the smallest sized fish (low-ration, slow-speed) had one of the lowest mortality rates.

Dry mass

Estimates of fish dry mass for each sample were obtained from mass-on-length regressions (Table 3) by using length estimates corrected for mortality in three feeding treatments (Table 2) and assuming no length change in the other treatments. In all but one case, the final dry mass estimates were significantly greater (high- and low-ration treatments) or lower (zero-ration treatments) than the initial estimates (t-test, $P \leq 0.05$). In the zero-ration treatments, the loss of dry mass was more than twice as rapid in the fast-speed treatments as it was in the slow-speed treatments (Table 3). Dry mass increased about four times more rapidly during the high-ration treatments than during the low-ration treatments, and dry mass increased more than twice as rapidly during slow-speed treatments as during fast-speed treatments at both rations. Dry mass did not change significantly between the initial and final estimates when fish were fed the low ration and swam at the fast speed, so growth was assumed to be zero (Table 3).

In three feeding treatments (Table 3) the increases in mass were dependent on estimated increases in length. Although realistic, the corrected length increases (Table 2) may not have been accurate. Therefore, conservative estimates of mass increases in the feeding treatments were calculated by assuming that there was no increase in length (Table 3). A significant length-specific increase over initial dry mass was found in the slow-speed, high-ration treatment.

Caloric growth and gross conversion efficiency

Fat content (Table 3) increased substantially during the high-ration treatments, wherein about 70% of the increase in dry mass was fat. Fat increased about twice as much in the high-ration, slow-speed treatment as in the high-ration, fast-speed treatment. No strong trends in percent fat were found in the low-ration treatments.

The average percent fat of each sample was used to calculate mass of fat and fat-free dry mass per fish. Then the total fish energy content for each sample was calculated (Table 3) by assuming heat of combustion values equal to 29 kcal/g for fat-free dry mass and 9.227 kcal/g for fat (Hunter and Leong 1981).

The trends in total energy content from all of the treatments (Fig. 4) were consistent with a simple energy budget in which more food energy taken in (R), or less energy required for metabolism (Q), results in more energy available for reproduction (S), growth (G), and fat storage (F):

$$R = Q + X + I + S + G + F \text{ cal.} \qquad (5)$$

Components of the energy budget that were not individually estimated were excretion (X) and digestive losses (I). No spawning occurred during the experiments, although gonad mass changed. In the following analyses, changes in gonad and somatic mass were combined as overall growth (B) and fat storage (F). Metabolism was separated into maintenance metabolism (Q_M) and the metabolism associated with extracting usable energy from food (SDA). Ninety percent of the energy losses during starvation were assumed to be respired (Q_M), with excretion accounting for the remainder. This is consistent with estimates of endogenous excretion given by Durbin and Durbin (1981, 1983). The "metabolizable fraction" of fasting energy losses has been assumed to be as little as 80% (Brett 1973) for energy derived from body protein. In the present study, about one-third to one-half of the calories lost during fasting were derived from protein.

Energy losses during fasting were greatest during the fast-speed treatment (28.2 cal · g fish wet mass^{-1} · day^{-1})** and lowest during the slow-speed treatment (17.6 cal · g^{-1} · day^{-1}, Fig. 4). Growth (in cal · g^{-1} · day^{-1}) was greater at both speeds when rations (R) were high than when they were low (Fig. 4). At both

** Hereafter the unit of mass (g^{-1}) refers to fish wet mass.

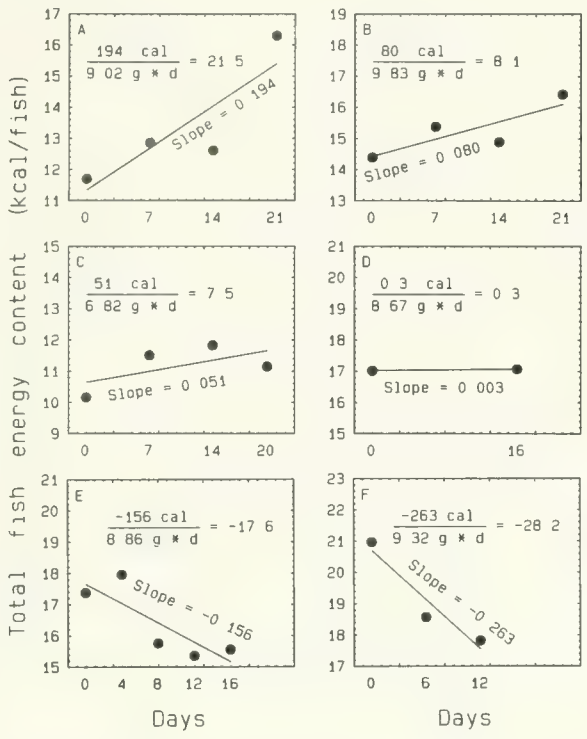

Figure 4

Estimated rates of changes in fish energy content. Slopes were converted into mass-specific rates of caloric growth at the high-ration level for (A) slow-swimming and (B) fast-swimming speeds and at the low-ration level for (C) slow-swimming and (D) fast-swimming speeds. Negative slopes from the zero-ration treatments were converted into mass-specific rates of energy loss for (E) slow-swimming and (F) fast-swimming speeds.

feeding levels, caloric growth was greater in the slow-speed than in the fast-speed treatments. In each treatment, energy utilization (in cal $\cdot g^{-1} \cdot day^{-1}$) not accounted for by maintenance metabolism (Q_M) and caloric growth (B+F) was a relatively constant fraction of the energy consumed:

	Ration (R)	–	Growth (B+F)	–	Maintenance (Q_M)	=	Excretion (X) + Digestive losses (I)	+ SDA
High ration, slow speed:	55.7	–	21.5	–	0.9(17.6)	=	20.1	= 0.36R
High ration, fast speed:	52.0	–	8.1	–	0.9(28.2)	=	18.5	= 0.36R
Low ration, slow speed:	37.6	–	7.5	–	0.9(17.6)	=	14.3	= 0.38R
Low ration, fast speed:	37.2	–	0.3	–	0.9(28.2)	=	11.5	= 0.31R

Mean 0.35R

About 35% of the food energy was lost through excretion (X), digestive losses (I), and SDA, so the energy budget Equation (5) may be simplified as

$$R = (B + F + Q_M) / 0.65 \text{ cal} \cdot g^{-1} \cdot day^{-1}. \quad (6)$$

Observed gross conversion efficiency (K) was calculated by dividing caloric growth (B + F) by ration (R). Gross conversion efficiency predicted by the energy budget approximation (Equation 6) was

$$K = \frac{R - (0.35\ R) - Q}{R} \text{ (dimensionless).} \quad (7)$$

The model closely matched the observed gross conversion efficiencies:

	Gross conversion efficiency (%)	
	Observed	Equation (7)
High ration, slow speed:	39	37
High ration, fast speed:	16	16
Low ration, slow speed:	20	23
Low ration, fast speed:	1	–3

These results indicate that a simple energy budget model, assuming a loss of 35% of the food energy due to X, I, and SDA, explains increased growth with increased ration and decreased growth with increased activity.

Discussion

Gross conversion efficiencies

The energy budget approximation (Equation 7) implies that gross conversion efficiency is reduced by low ration and high activity. This was supported by the lower

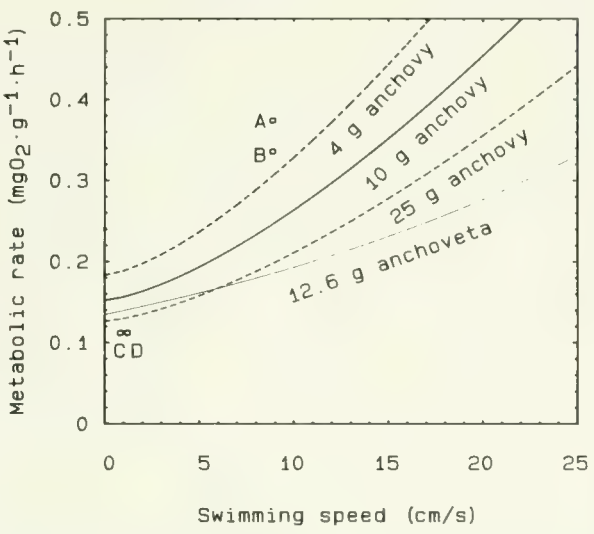

Figure 5

Comparison of other engraulid metabolic rate estimates with model predictions for 4, 10, and 25 g northern anchovy at 17°C. The anchoveta curve is from Villavicencio (1981, temp. 17°C). Respiration rates of (A) actively swimming 10 g northern anchovy at 15°C and, based on energy losses during zero-ration treatments, (B) exercised 16.9–17.8 g fish at 21°C, (C) non-exercised 13.5–16.9 g fish at 18°C, and (D) non-exercised 12.3 g fish at 15.2°C as measured by Kaupp et al. (unpubl. data).

K values in treatment combinations with low ration or high speed compared with the high-ration, slow-speed treatment. Contrarily, K values in the high-ration, slow-speed treatment were much higher than the 12.8% reported by Hunter and Leong (1981) for northern anchovy even though the fish in the present study were exercised and fed smaller rations. Hunter and Leong (1981) fed fish 124 cal $\cdot g^{-1} \cdot day^{-1}$ of semi-dry, pelleted trout food (the caloric equivalent of a ration of 16% of wet body mass/day in copepods). At very high rations, the proportion of food energy lost to X, I, and SDA may increase (Paloheimo and Dickie 1966, Brett 1979, Brett and Groves 1979), causing K to decline.

The euphausiids used for food and the rations (Table 1) in the present study were similar to the zooplankton rations of 1.4–4.9% observed in nature (Blaxter and Hunter 1982). So, although X, I, and SDA vary with food composition (Elliott 1976b, Brett and Groves 1979, Tandler and Beamish 1979 and 1980) and may increase at ration levels higher than those in nature, the energy budget generalizations in Equations (6) and (7) should be applicable to adult anchovy in the wild.

The observed range of gross conversion efficiencies (1–39%) extended higher than the range reported for clupeoids (7–13.5%, Takahashi and Hatanaka 1960, De Silva and Balbontin 1974, Hunter and Leong 1981, Blaxter and Hunter 1982). However, gross conversion efficiencies this high are found in many juvenile fishes (60% Hatanaka and Takahashi 1956, 34% Elliott 1976a, 10–25% Brett and Groves 1979). The importance of different results in such studies is difficult to judge, because of differences in the assumptions, expressions (percentages of mass or energy), experimental conditions (size, maturity, temperature, activity), and the rarity of error estimates.

A model for adult anchovy metabolism

A model for anchovy metabolism was derived by using the estimates from the present study, data on closely related species, and general principles relating swimming speed and metabolism to fish size. The model required estimates of (1) standard metabolism, (2) swimming metabolism, (3) the effect of fish size on standard and swimming metabolism, and (4) the effect of temperature. These estimates are provided in the following sections.

Standard metabolism Standard metabolism was estimated by extrapolating to zero swimming speed from the rates estimated at two speeds. An exponential relationship (Brett 1964) was assumed,

$$Q_M = ae^{bV} \text{ cal} \cdot g^{-1} \cdot day^{-1}, \quad (8)$$

where the metabolic rate exclusive of SDA (Q_M) consists of standard metabolism (Q_0 = a) increased by a factor (e^{bV}) for the cost of swimming, where V is swimming speed. The energy losses measured in the present study resulted from fish exercising half the time and resting half the time, so

$$Q_M = [0.5\ (ae^{bV})] + [0.5\ (a)] \text{ cal} \cdot g^{-1} \cdot day^{-1}. \quad (9)$$

The metabolic rate estimates ($Q_M = 0.9 \times 17.6 = 15.8$, and $0.9 \times 28.2 = 25.4$ cal $\cdot g^{-1} \cdot day^{-1}$) from the two exercise levels (V = 8.7 and 21.1 cm/s, respectively) were substituted for Q_M and V in Equation (9). The resulting simultaneous equations were solved, and Q_0 was calculated to be 12.1 cal $\cdot g^{-1} \cdot day^{-1}$ at V = 0. Assuming an oxycalorific equivalent of 3.24 cal/mg O_2 (Elliott and Davison 1975), the standard metabolic rate was 0.156 mg $O_2 \cdot g^{-1} \cdot h^{-1}$. Assuming the same metabolizable fraction (0.9) and oxycalorific equivalent, energy losses of 9.7 cal $\cdot g^{-1} \cdot day^{-1}$ at the lowest activity levels measured by S. Kaupp et al. (unpubl. data,) amounted to 0.112 mg $O_2 \cdot g^{-1} \cdot h^{-1}$. The standard metabolism of 12.6 g anchoveta at 17°C (Villavicencio 1981) was 0.135 mg $O_2 \cdot g^{-1} \cdot h^{-1}$. These values (Fig. 5)

were similar to the estimate of Q_M in the present study.

Swimming metabolism Standard metabolism (Q_0 = 12.1 cal · g^{-1} · day^{-1}) subtracted from the Q_M estimates for fish at the two speeds left 3.7 and 13.3 cal · g^{-1} · day^{-1}, respectively, for the metabolic cost of swimming (Q_V) for 12 hours a day at 8.7 and 21.1 cm/s. On an hourly basis, Q_V amounted to 0.308 and 1.11 cal · g^{-1} · h^{-1}, respectively. A linear fit to log-transformed estimates of Q_V versus log-transformed V indicated that

$$Q_V = (0.0137\ V^{1.44})\ \text{cal} \cdot \text{g}^{-1} \cdot \text{h}^{-1}. \quad (10)$$

For extrapolating beyond the range of measurements, a power function makes a good model for swimming metabolism, because mechanical principles and empirical evidence (Ware 1978, Wu and Yates 1978) indicate that thrust and drag in swimming fish are power functions of speed.

Effect of fish size Fish size was not manipulated in the present study, so size effects could not be quantified from the results. However, reviews (Winberg 1956, Brett and Groves 1979) of results from a large number of studies have led to the generalization that the mass exponent of standard metabolism in fishes is close to 0.8. The corresponding mass-specific exponent (−0.2) combined with the estimate of Q_0 from the present study results in this model,

$$Q_0 = 18.8\ M^{-0.2}\ \text{cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$$

$$= 0.783\ M^{-0.2}\ \text{cal} \cdot \text{g}^{-1} \cdot \text{h}^{-1}, \quad (11)$$

where M is anchovy wet mass (~9g in the present study).

The effect of fish size on the cost of swimming can be modeled by expressing speed relative to length so that the cost of swimming at the normalized speed is the same for any size of fish. The cost of swimming in sockeye salmon *Oncorhynchus nerka*, obtained by subtracting standard metabolism from total metabolism of 8–54 cm salmon swimming at speeds of 13–143 cm/s (Brett 1965), can be accurately described by a power function of the Reynolds number (Wu and Yates 1978). The Reynolds number combines fish length, speed, and kinematic viscosity. A similar way of expressing this relationship, which matches Brett's (1965) results (at 15°C) extremely closely, is

$$Q_V = 8.7934 \left(\frac{V}{L^{0.64}}\right)^{1.71}\ \text{mg}\ O_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}. \quad (12)$$

Thus, for different sizes of sockeye salmon, the cost of swimming is the same when speed (V) divided by fish length (L in cm) to the 0.64 power is the same. This relationship is also reflected in length exponents (0.5–0.7) for endurance speed in fishes (Bainbridge 1962, Hunter 1971). Note that dividing V by L (body lengths/second) does not normalize speed with respect to swimming cost or endurance. For anchovy, the present study assumed that the length exponent for normalized speed was 0.6. Then, from Equation (10)

$$Q_V = 0.095 \left(\frac{V}{L^{0.6}}\right)^{1.44}\ \text{cal} \cdot \text{g}^{-1} \cdot \text{h}^{-1}, \quad (13)$$

and the cost of swimming in anchovy can be estimated for any size and swimming speed.

Effect of temperature Anchovy metabolic rates were estimated at only one temperature (17°C) in the present study, but the effect of temperature on engraulid anchovy metabolism was estimated for Peruvian anchoveta (Villavicencio 1981) at 14–20°C. These data indicated an increase of 78% in total respiration rate over a change of 6°C. Applying this intensity of temperature effect to the model would amount to

$$Q' = 2.046\ Q\ e^{0.0959\ T}\ \text{(in any units)}, \quad (14)$$

where Q is the metabolic rate (in any units) at 17°C, and T is the ambient temperature (°C). However, short-term temperature acclimation periods in the laboratory (Villavicencio 1981) may result in greater metabolic rate changes than in the long term in nature. Estimates from Equation (14) should be viewed skeptically, until better estimates of the effect of temperature on anchovy metabolism can be found.

Evaluation of the model

Estimates of maintenance metabolism ($Q_M = Q_0 + Q_V$) from the model (Equations 11 and 13) for 4, 10, and 25g northern anchovy at 17°C were compared with other data on engraulids (Fig. 5), assuming an oxycalorific equivalent of 3.24 cal/mg O_2 (Elliott and Davison 1975). Oxygen consumption of northern anchovy swimming at about 9 cm/s in an annular respirometer was 0.38 mg O_2 · g^{-1} · h^{-1} (Kaupp et al. unpubl. data). The rate of energy loss in fasting northern anchovy swimming in a flume at about 9 cm/s was 29.3 cal · g^{-1} · day^{-1} or 0.34 mg O_2 · g^{-1} · h^{-1} (Kaupp et al. unpubl. data, energy loss multiplied by 0.9, the metabolizable fraction). These data were about twice as high as the tunnel respirometry data on anchoveta (Villavicencio 1981) swimming at 9 cm/s (Fig. 5). The model

predicts metabolic rates in the middle of this range, indicating that it may provide reasonable estimates for engraulid metabolism.

To use the model to estimate ration, the energy required for standard metabolism (Equation 11) and the cost of swimming (Equation 13 converted to cal $\cdot g^{-1} \cdot day^{-1}$) plus the energy needed for growth or reproduction, are multiplied by 1/0.65 (from Equation 6) to account for X, I, and SDA. The result is the daily food energy requirement. Similarly, 65% of food energy minus standard and swimming metabolism gives the surplus available for growth and reproduction at that level of food intake and activity.

Hunter and Leong (1981) estimated the food energy requirements of 1-year-old anchovy (wet mass 10.3 g, length 10.3 cm) at 33.8 cal $\cdot g^{-1} \cdot day^{-1}$ (copepods at 4% of wet mass/day). According to the model in the present study, X, I, and SDA remove 11.8 cal $\cdot g^{-1} \cdot day^{-1}$, and standard metabolism (Equation 11) is 11.8 cal $\cdot g^{-1} \cdot day^{-1}$. Supposing 1-year-old anchovy swim at 12 cm/s for 12 hours each day, this costs 0.45 cal $\cdot g^{-1} \cdot h^{-1}$ (Equation 13), or 5.4 cal/g. If they swim at 2 cm/s for the other 12 hours, this costs another 0.4 cal/g, making the total swimming cost 5.8 cal $\cdot g^{-1} \cdot day^{-1}$. Subtracting all these costs from the ration energy leaves 4.4 cal $\cdot g^{-1} \cdot day^{-1}$, which Hunter and Leong (1981) estimated to be enough for normal growth plus 20 spawnings per year.

Is this level of swimming activity realistic? Using sonar tracking and Doppler shift analysis, Holliday (1977) measured a relatively uniform swimming speed averaging 45 cm/s over a 40-minute interval for what were thought to be northern anchovy about 14 cm long (25 g). To swim for 12 hours a day at this speed, while maintaining normal growth and spawning 20 times per year, 3-year-old anchovy (Hunter and Leong 1981) would require a ration of 7.7% of body weight per day. However, 3 hours a day at this speed, with the rest of the day at 3 cm/s, would allow for the same growth and reproduction on a ration of only 4%.

It appears that anchovy growth rates in nature and the estimate of spawning 20 times per year (Hunter and Leong 1981) are consistent with the current study's model predictions for anchovy swimming at speeds and consuming rations similar to those observed in nature. Three aspects of the model were determined by experiment: (1) A constant proportion of food energy is available for metabolism and growth, (2) metabolism increases with swimming speed, and (3) gross energy conversion efficiency is a function of ration level and activity. The model should be useful in estimating the effect of changing food abundance on spawning frequency and growth, particularly as more measurements of activity become available.

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Abstract.—Laboratory experiments were conducted to determine how growth and survival of early-life-history stages of California halibut *Paralichthys californicus* are influenced by temperature, and how optimal temperature ranges may change with ontogeny. As halibut developed from eggs to juveniles, highest survival occurred at increasingly higher temperature ranges. Within tolerance limits, growth and development rates of all early-life-history stages were directly proportional to temperature. Eggs hatched successfully at 12, 16, and 20°C; at 8 and 24°C they died prior to embryo formation. Larval survival 17 days after hatching was 23–46% at 16, 20, and 24°C, but almost all larvae died at 12°C after an initial period of high survival. At 8°C, larval development ceased at the early yolksac stage. Survival of 3-month-old juvenile halibut was significantly greater at 20, 24, and 28°C (57–76%) than at 16°C (31%). Temperature also affected settlement rate; when the temperature of 1-month-old larvae was raised from 16°C to 20°C, settlement occurred about a week sooner than settlement of larvae remaining at 16°C. Tolerance ranges of halibut early-life-history stages determined in the laboratory approximate temperatures encountered by halibut in the field; high densities of newly-settled halibut larvae and juveniles have been collected in shallow areas of bays where temperatures are often higher than the open ocean inhabited by young larvae. These warmer inshore nursery grounds could enhance growth and survival of halibut juveniles.

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Effects of Temperature on Early-life-history Stages of California Halibut *Paralichthys californicus*

Dena M. Gadomski

VANTUNA Research Group, Occidental College
1600 Campus Road, Los Angeles, California 90041
Present address: National Fishery Research Center — Columbia River Field Station
U.S. Fish and Wildlife Service, Star Route, Cook, Washington 98605

Steven M. Caddell

Section of Ichthyology, Natural History Museum of Los Angeles County
900 Exposition Boulevard, Los Angeles, California 90007
Present address: GATX, 2000 E. Sepulveda Boulevard, Carson, California 90810

The California halibut *Paralichthys californicus* (family: Paralichthyidae) is important to commercial and recreational fishermen in central and southern California. Adult halibut spawn in nearshore waters (Frey 1971, Lavenberg et al. 1986) and eggs hatch in about 2 days at 16°C (Gadomski et al. 1990). Lavenberg et al. (1986) collected halibut larvae year-round within the 75 m contour of the Southern California Bight, with greatest abundance during winter and spring. When larvae are about 1-month-old and 8 mm standard length, they metamorphose and settle to the bottom (Allen 1988, Gadomski et al. 1990). Although spawning has not been observed in bays and estuaries, high densities of newly-settled halibut larvae and juveniles have been collected in these areas, often in waters as shallow as one meter (Allen 1988, Kramer 1990). It is not known at what stage of development inshore movement occurs, and whether the mechanism of transport is passive or active. The advantages of estuarine nursery areas for juvenile fishes have been often cited (McHugh 1967, Pearcy and Myers 1974, Boehlert and Mundy 1988). Estuaries commonly have greater food availability and protection from predation and adverse weather conditions.

As early development progresses, halibut may experience an increasingly higher range of temperatures due both to the distribution changes described above and to seasonal temperature differences. When eggs and young larvae are in nearshore waters of southern California during winter and spring, typical surface temperatures are about 13–17°C (Petersen et al. 1986). Juveniles in inshore waters during summer months commonly experience temperatures above 20°C, and shallow areas may be as warm as 24°C (Kramer 1990). Thus, one advantage of inshore migration might be higher temperatures, which could result in enhanced juvenile growth.

Fishes generally have temperature ranges at which growth and survival are optimum. These may differ with age; young of some species prefer warmer temperatures than adults (Norris 1963, McCauley and Huggins 1979). Early-life-history stages may also have different optimal temperatures, which may reflect field temporal and spatial distributions. For example, sole *Solea solea* larvae from North Sea coastal regions require

higher temperatures for successful development than sole eggs, probably because sole's spring spawning cycle results in larval abundances later in the season when sea temperatures are warmer (Irvin 1974, Fonds 1979).

Our purpose was to determine how growth and survival of California halibut may be influenced by temperature during development from egg to 3-month-old juvenile, and how optimal temperature ranges may change with ontogeny. Additionally, we were interested in how temperature may influence the timing of an important stage of flatfish development—settlement. We examined the possibility that month-old pelagic larvae passively transported to warmer inshore waters would settle significantly sooner due to a faster development rate than those remaining in colder offshore areas, resulting in selective settlement of shallow coastal nursery grounds. Larvae remaining pelagic due to colder waters would have a continued chance of transport inshore. The results of this study will aid in better understanding how oceanographic conditions may influence the survival of halibut early-life-history stages in the field.

Methods

Egg development

Eggs and sperm were stripped from ripe field-collected California halibut and combined in petri dishes. Approximately 300 fertilized eggs were placed in each of ten 3 L glass jars containing filtered, ultraviolet-light sterilized seawater (35‰) at an ambient temperature of 16°C. To establish and maintain desired temperatures, jars were placed in temperature-controlled water baths. A low level of aeration was provided in each jar to avoid the formation of temperature gradients. Soon after fertilization, temperatures in eight jars were raised or lowered 1°C/15 minutes from 16°C to 8, 12, 20, and 24°C, resulting in two replicates of each temperature treatment. Light cycles simulated natural conditions (12L:12D). Every 2 hours until hatching, temperatures were recorded and at least five live eggs were sampled from each jar and preserved in 4% formalin. Because of the short experimental duration, water in the jars was not exchanged with fresh seawater during the experiment; when eggs in all jars had hatched or died, the experiment was terminated. To monitor development, egg series were examined using a dissecting microscope.

Larval growth and survival

An experiment was initially conducted to determine the influence of temperature on starvation rate of newly-hatched halibut larvae. Fertilized eggs were obtained from natural spawns from brood stock held in an outdoor 5 m diameter tank with a flow-through seawater system (for a further description of brood stocks, see Caddell et al. 1990). Seventy-five late-stage eggs (with developed embryos) were placed in each of ten 3 L glass jars of sterilized seawater at an ambient temperature of 16°C. Jars were in temperature controlled water baths and light aeration was provided. Temperatures in eight jars were raised or lowered 1°C/15 minutes from 16°C to 8, 12, 20, and 24°C; each temperature treatment was replicated. Light cycles simulated natural conditions (12L:12D). Twenty percent of the water volume was replaced with fresh seawater twice weekly; at this time, ammonia and salinity levels were monitored. Dead halibut larvae were removed and counted daily until total starvation had occurred.

To determine how growth and survival of halibut larvae are temperature-dependent, the above experiment was repeated except food was added. Gadomski and Petersen (1988) found that for greatest survival, first-feeding halibut required food by the day of total yolk absorption. Full yolk depletion occurs 6 days after hatching at 16°C, but yolk absorption time varies with temperature (Gadomski et al. 1990). In the current study, we fed rotifers *Brachionus plicatilis* to halibut larvae after eye pigmentation and mouth development, but before total yolk absorption. Rotifers were stocked at 15/mL, following the methods of Gadomski et al. (1990), and supplemented thereafter as needed to maintain this density. Dead halibut larvae were removed and counted daily. Seventeen days after hatching, notochord lengths of surviving larvae were measured.

Because final survival was the same (zero) for all starvation trials, we compared survival curves of starved and fed larvae using the Mantel-Haenszel test (Matthews and Farewell 1985, Gadomski and Petersen 1988). This method tests the null hypothesis that incremental survival rates, computed between successive sampling times, are similar throughout the observation period. Rapid decomposition of deceased larvae resulted in accumulative totals of survivors and mortalities in some trials at the end of the experiment to be less than the original stocking density of 75. The Mantel-Haenszel test compensated for this by adding the "lost" mortalities to each experimental day proportionate to the known number that had died that day. First we tested if replicates could be combined; then we tested for a significant difference between survival curves of each experiment (starved and fed): 12°C vs. 16°C, 16°C vs. 20°C, and 20°C vs. 24°C. Because of

their similarity, survival curves of 12°C starved and 12°C fed trials were additionally compared.

For the fed trials, analysis of variance (ANOVA) was used to test for significant differences in final survival [ln(number alive + 1)] and also differences in mean larval length between temperatures; if significant differences were found, Duncan's multiple range test was applied.

Juvenile growth and survival

Twenty-five 30-day-old pelagic larvae, which had been held at a mean ambient temperature of 16.7°C (SE 0.1), were stocked in each of twelve indoor 15 L black fiberglass tanks (40 cm diam., 12 cm depth) at 16°C. Water quality was maintained using a slow-drip flow-through system and tank aeration; ammonia and salinity levels were monitored weekly. A natural cycle of light and dark (12L:12D) was provided. Temperatures were raised using aquarium heaters in nine tanks 0.5°C per day from 16°C to 20, 24, and 28°C, resulting in three replicates per temperature. Fish were fed rotifers and newly-hatched brine shrimp nauplii (*Artemia* sp.) to excess. Dead fish were removed and counted daily and, in the last 15 days of the experiment, measured if not badly decomposed. The experiment was terminated when fish were 97 days old; survivors were counted and standard lengths determined. ANOVA and Duncan's multiple range test were utilized to test for significant differences in final survival and size between temperatures. Student's t-test was used to test for significant differences in mean standard lengths between 16°C and 20°C mortality and survivor groups.

Larval settlement

The settlement rate of a group of larvae held constantly at 16°C was compared with that of a group of larvae from the same cohort exposed to 20°C when a month old. These two temperature regimes were designed to simulate temperatures halibut larvae would encounter in the field if they (1) remained in colder offshore waters, or (2) were transported to warmer inshore areas when a month old.

Fifteen 30-day-old pelagic larvae that had been held at a mean temperature of 15.9°C (SE 0.1) were transferred to each of six indoor 15 L black fiberglass tanks at 16°C. Temperatures were raised 2°C a day to 20°C in three of the tanks while keeping three tanks at 16°C. Light cycles simulated natural conditions (12L:12D). Tanks were aerated to maintain water quality and avoid the formation of temperature gradients. Three times a week, 20% of the volume of water in each tank was replaced with fresh seawater; at this time, salinity and ammonia levels were monitored. Larvae were fed rotifers and newly-hatched brine shrimp to excess. Dead larvae were removed and counted daily. Each tank was observed for 10 minutes twice daily (morning and afternoon) and the numbers of settled and pelagic larvae counted; the mean values of these two daily observations were used to calculate percent settled larvae per tank per day. We defined "settled" larvae to be individuals that remained on the tank bottom (on their side) for at least 5 seconds during an observation period. This behavior occurs before metamorphosis is complete (Gadomski et al. 1990). When 100% settlement was observed in all tanks, fish were removed and standard lengths determined. Student's t-test was utilized to test for a significant difference in mean fish lengths between temperature treatments.

Results

Egg development

Halibut eggs are buoyant and about 0.8 mm in diameter with a single 0.14 mm oil globule. Eggs developed to hatching at 12, 16, and 20°C (Table 1). At 8°C, eggs did not develop beyond the 32-cell stage, and at 24°C cell divisions were abnormal and ceased during early development. Time to hatching was inversely propor-

Table 1

Egg development rates of California halibut *Paralichthys californicus* at five temperatures. Times (hours) after fertilization at which developmental events (I–VII) were first observed are presented. Two replicate jars were maintained at each temperature, with initially 300 recently-fertilized eggs per replicate; every 2 hours until hatching, at least five live eggs were sampled from each jar and egg development noted.

		Hours post-fertilization				
	Mean temp. (°C):	8.4	12.4	16.0	20.8	23.9
	SE (°C):	(0.2)	(0.1)	(0.1)	(0.1)	(0.6)
I	2–128 cells	4	4	2	2	2
II	Multicelled blastodermal cap	Dead	10	8	6	6
III	Germ ring >1/2 down yolk mass		26	18	14	Dead
IV	Embryo visible		32	22	16	
V	Blastopore closed		34	24	18	
VI	Tail separated from yolk mass		52	38	26	
VII	Eggs hatched		74	50	34	

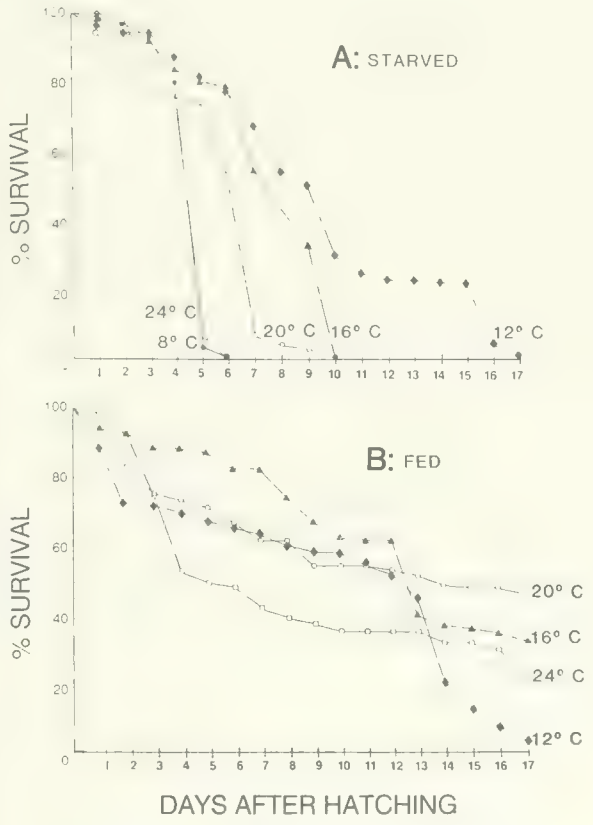

Figure 1

Survival (%) over a 17-day period of California halibut *Paralichthys californicus* larvae subjected to various temperatures. Groups of larvae were either (A) starved or (B) fed rotifers. Points are replicates (n 2) combined. Each replicate originally consisted of 75 individuals. The fed experiment did not include an 8°C trial because larvae at 8°C did not develop functional mouths or eyes and died with undepleted yolksacs.

tional to temperature: 74, 50, and 34 hours at 12, 16, and 20°C, respectively. Although not quantified, most eggs remaining (the initial number was reduced by sampling) at each temperature hatched. No abnormal yolksac larvae were observed.

Larval growth and survival

Replicates (n 2) of survival curves at each temperature for starved and fed larvae were combined for analysis since they were not significantly different ($P<0.05$). Survival curves of 12, 16, 20, and 24°C starved trials were significantly different ($P<0.01$), with starvation time (6–17 days) inversely proportional to temperature (Fig. 1A). Total mortality occurred first at temperature extremes, 8 and 24°C, which had similar mortality curves. Larval development at 8°C never progressed beyond the yolksac stage with unpigmented eyes and nonfunctional mouths (thus the fed experiment did not include an 8°C trial). At 24°C, however, dead larvae had pigmented eyes, functional mouths, and completely depleted yolks.

Survival curves of 20 and 24°C fed larvae were statistically similar, while the 12 and 16°C fed trials differed ($P<0.05$). At 24°C, mortality initially was high, perhaps due to temperature acclimation problems, but then mortality was gradual, paralleling the 20°C curve. At 16°C, survival initially was highest, but dropped after 12 days. Survival was high for fed larvae at 12°C until the end of the second week when the mortality rate increased, resulting in almost total mortality by day 17 (Fig. 1B). Although this survival pattern approximates the starved 12°C counterpart, the two curves are significantly different ($P<0.01$; more larvae in the fed trial survived longer). Fed larvae at 12°C initiated feeding (since food was observed in their guts) but survival enhancement was only short-term.

Final survival of fed larvae at 16°C was intermediate to final survival values at 20°C and 24°C; final survival was highest at 20°C and nearly zero at 12°C (Fig. 1B). Final survival did not significantly differ between temperature treatments (P 0.14), however. At experimental end, mean notochord lengths of surviving fed larvae were directly proportional to temperature (Table 2) and significantly different between all temperatures ($P<0.05$).

Table 2

Mean notochord lengths of larval California halibut *Paralichthys californicus* 17 days after hatching at four temperature treatments. Two replicates were maintained at each temperature, with initially 75 late-stage eggs per replicate. N = combined number of surviving larvae in the two replicates.

Temperature (°C)			Notochord length (mm)	
Mean	SE	N	Mean	SE
12.3	(0.2)	4	3.92	(0.09)
16.2	(0.1)	45	4.80	(0.07)
20.0	(0.1)	69	5.31	(0.07)
24.1	(0.1)	34	5.94	(0.03)

Juvenile growth and survival

Replicates (n 3) did not differ and were combined for analysis. Survival of 97-day-old fish at 16°C was significantly ($P<0.05$) lower than survival at 20, 24, or 28°C (Fig. 2); there were no significant survival differences between the three higher temperatures. Final mean standard length at 16°C did not differ signif-

Table 3

Mean standard lengths of 97-day-old juvenile California halibut *Paralichthys californicus* at four temperature treatments (acclimated when 1 month old from 16.7°C). Three replicates were maintained at each temperature, with initially 25 larvae per replicate. N = combined number of surviving juveniles in the three replicates.

Temperature (°C)			Standard length (mm)	
Mean	SE	N	Mean	SE
16.1	(0.1)	23	18.48	(0.93)
19.7	(0.0)	57	18.10	(0.39)
23.7	(0.1)	43	24.24	(0.57)
27.5	(0.0)	55	26.92	(0.71)

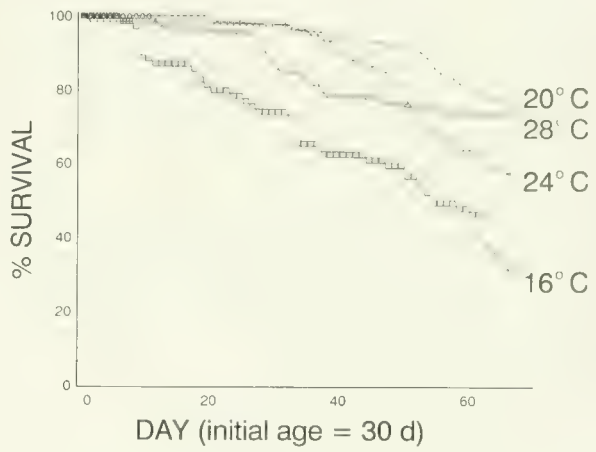

Figure 2

Survival (%) over a 67-day period of California halibut *Paralichthys californicus* larvae and juveniles at four temperatures. Larvae held at 16.7°C were transferred into experimental containers when 30 days old. Points are replicates (n 3) combined. Each replicate initially consisted of 25 larvae.

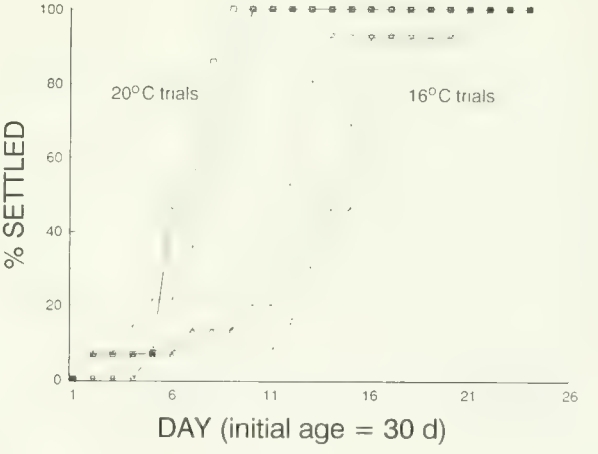

Figure 3

Percent of California halibut *Paralichthys californicus* settled per day at 16°C and 20°C. Larvae held at 16°C were transferred into experimental containers when 30 days old. Three replicate trials were conducted at each temperature. Each replicate initially consisted of 15 larvae.

icantly from 20°C ($P<0.05$), but final mean length was significantly larger at 24°C, and larger at 28°C than 24°C (Table 3). These results were unexpected, since all previous experiments have demonstrated greater growth at 20°C than 16°C (Gadomski et al. 1990). Measurements of dead fish removed during the last 15 days of the experiment, however, indicated that smaller individuals were dying at 16°C than at 20°C, which biased the final growth data. Mean standard lengths at 16°C of fish that died during two time periods—the five (days 63–67) and fifteen (days 53–67) day intervals before the end of the experiment—were similar, 12.68 mm (SE 0.77, n 8) and 12.57 mm (SE 0.49, n 14), respectively, and were significantly smaller ($P<0.01$) than mean mortality lengths at 20°C for these same two time periods, 17.46 mm (SE 2.02, n 3) and 16.21 mm (SE 1.12, n 8). The mean standard length (12.68 mm, SE 0.77, n 8) of fish that died near the end of the experiment (days 63–67) at 16°C was also significantly smaller ($P<0.05$) than the final mean standard length of surviving individuals at 16°C, 18.48 mm (SE 0.93, n 23), indicating that size-selective mortality had occurred.

Larval settlement

There were no significant differences in survival between temperatures ($P<0.01$), with individual tank survival ranging from 80% to 93%. Larvae settled sooner at 20°C (actual mean temperature 20.0°C, SE 0.0) than 16°C (15.8°C, SE 0.1) (Fig. 3). At 20°C, 50% had settled by 6–8 days after transfer from 16°C, and all were settled by 10 days after transfer (when 40 days old). In contrast, at 16°C, 50% settlement did not occur until 12–15 days after transfer, and the last few larvae did not settle until 21–22 days (when 51–52 days old).

At the end of the experiment, larvae held at 20°C were significantly larger ($P<0.01$) than those at 16°C. At the beginning of the experiment (when transferred from 16°C), 30-day-old larvae had a mean length of 6.74 mm (SE 0.10, n 15) with 80% still exhibiting incomplete notochord flexion [the remaining 20% had achieved full flexion (standard length)]. All exhibited full elongation of the second to sixth dorsal rays

[dorsal ray elongation is characteristic of larvae of many pleuronectiform fishes; rays regress during metamorphosis (Ahlstrom et al. 1984, Gadomski et al. 1990)], and no eye migration was evident. At experimental end, 53-day-old larvae at 16°C had a mean length of 8.75 mm (SE 0.16, *n* 38), while at 20°C, mean larval length was 12.88 mm (SE 0.23, *n* 40). All fish at both temperatures had achieved standard length and had fully migrated eyes. Those at 16°C were somewhat less developed, however, since 8% still had slightly elongated dorsal rays. The remainder at 16°C and all fish at 20°C exhibited normal length dorsal rays characteristic of juveniles.

Discussion

Temperature tolerance experiments have been conducted on eggs and larvae of many fish species (Houde 1974, Laurence and Rogers 1976, Laurence 1978, Ferraro 1980, Bolla and Holmefjord 1988). The temperature tolerance range of California halibut eggs in the current study was at least 8 degrees (12–20°C), and probably more if the range endpoints fell between 8–12°C and 20–24°C. This 8-degree range is typical of other flatfish species such as English sole *Parophrys vetulus*, sole *Solea solea*, and winter flounder *Pseudopleuronectes americanus* (Alderdice and Forrester 1968, Irvin 1974, Fonds 1979, Buckley 1982). Absolute temperatures tolerated varied among species, however, and were reflective of field habitat temperatures; sole *S. solea* eggs survived slightly lower temperature exposures than halibut (8–16°C), whereas English sole and winter flounder eggs (found in colder waters) tolerated much lower temperatures, 4–12°C and 2–10°C, respectively.

Temperature tolerance ranges may change with ontogeny. Halibut larvae exhibited a higher temperature tolerance range (16–24°C) than halibut eggs, a pattern which has also been demonstrated for sole *S. solea* (Irvin 1974, Fonds 1979) and yellow perch *Perca flavescens* (Hokanson and Kleiner 1974). Additionally, sole (Devauchelle et al. 1987) and yellow perch (Hokanson and Kleiner 1974) temperature tolerances were higher for late-stage eggs than for eggs at early developmental stages. Similarly in our study, larval halibut experiments initiated with late-stage eggs resulted in a higher range of temperature tolerance than experiments initiated with recently fertilized eggs. As larval halibut development progressed, temperature tolerance ranges also increased; soon after hatching, the highest mortality rate occurred at 24°C, whereas mortality of older larvae was greater at 12°C and 16°C (Fig. 1B).

At low temperatures, biochemical reactions, and thus metabolic rates and growth, of poikilotherms are reduced (Laurence 1975). For all halibut early-life-history stages, the lowest tested temperatures adversely affected growth and survival. Larval halibut may have a minimum necessary growth rate for survival, as suggested by Gadomski and Petersen (1988), and reported for larvae of other fish species (Jones 1973, Beyer and Laurence 1980, Govoni et al. 1986). At 8°C, development of halibut larvae halted soon after hatching when larvae still had significant amounts of yolk, unpigmented eyes, and nonfunctional mouths. Ehrlich and Muszynski (1982) found that at low temperatures, yolk-sac California grunion *Leuresthes tenuis* encountered problems with fat metabolism. At 12°C, survival of fed halibut larvae initially was high and ingestion was observed, but by 17 days after hatching almost all larvae were dead. This type of survival pattern was also reported by Laurence (1975) for winter flounder *Pseudopleuronectes americanus*, which survived in the laboratory at 2°C for 5 weeks with a very slow development rate, and then died before metamorphosis; larvae at higher temperatures of 5 and 8°C developed normally. Similarly, Laurence (1978) found that larval cod *Gadus morhua* and haddock *Melanogrammus aeglefinus* could only survive for limited periods after hatching at lower tested temperatures, with variable and elevated oxygen consumptions indicating physiological stress.

The temperature tolerance ranges of halibut eggs and larvae in the laboratory approximate temperatures these stages usually encounter in the field; deviations from normal sea temperatures could affect survival. During winter and spring, nearshore (1–20 km from shore) sea surface temperatures off southern California usually range between 13 and 17°C (Petersen et al. 1986). Vertical mixing during the winter season generally produces uniform temperatures throughout the water column. In late-spring and summer, surface waters warm as high as 20–22°C, and a thermocline develops (Petersen et al. 1986). Late-spring and summer upwelling events may disrupt this temperature stratification, however, transporting deep colder waters to the surface (Dorman and Palmer 1981). Our study has shown that halibut larvae can endure 12°C for a short period during the first 3 weeks after hatching, but years with prolonged periods of this temperature might result in high larval mortality. Since 1920, there have been only three instances when surface temperatures at the Scripps Pier off San Diego remained below 12.5°C for as long as 2 weeks, and these were all in the time period of December–February (E. Stewart, Scripps Inst. Oceanogr., La Jolla, CA). Temperatures considered lethal for halibut eggs and larvae (≤8°C) were never recorded at this site. In

contrast, areas north of Point Conception, California commonly have extended periods of temperatures below 12°C (SIO 1955–85, Parrish et al. 1981). Low northern California ocean temperatures may possibly limit the geographic range of larval halibut abundance, although areas off northern California are also characterized by strong offshore surface transport (due to upwelling), which in itself limits survival of pelagic fish eggs and larvae (Parrish et al. 1981).

Growth and development rates of halibut eggs and larvae in the laboratory increased with temperature increase. We did not determine the upper temperature tolerance limit of halibut larvae, but the highest temperature tested, 24°C, exceeds normal southern California ocean temperatures. Swift development of pelagic eggs and larvae in the field may be advantageous, since these stages are particularly vulnerable to predation (Bailey 1981). Conversely, faster development requires that more food be available, or starvation may quickly occur; we found that newly-hatched halibut larvae died sooner from starvation at higher temperatures (Fig. 1A), since yolk absorption was faster. Thus, warm ocean temperatures would increase starvation-related mortality of larval halibut in the field during periods with inadequate available food, while cold temperatures might decrease mortality.

Juvenile halibut had a higher temperature tolerance range than halibut eggs and larvae; survival of 3-month-old halibut was significantly lower at 16°C than at 20–28°C. Juvenile growth rates at 20, 24, and 28°C were directly proportional to temperature. Surviving juveniles were similarly sized at 16°C and 20°C (Table 3), but this final size data are biased because fish that died at 16°C were significantly smaller than those that died at 20°C. The less robust, slower-growing fish at 16°C died, perhaps indicating that young juveniles, like larvae (Laurence 1977, Houde and Schekter 1980), require a minimum growth rate for survival that was unattainable for some individuals at 16°C.

The higher temperature range required for best survival of juvenile halibut reflects observed spatial and temporal distribution patterns. High densities of newly-settled larval and juvenile halibut have been collected during spring and summer in southern California bays where waters may be as warm as 24°C (Allen 1988, Kramer 1990); solar heating of very shallow waters could result in even higher temperatures. Juveniles in shallow areas of bays and estuaries may thus have the advantage of enhanced growth and survival due to warmer waters, in addition to other advantages, such as increased food availability and protection. Larval cohorts that settle and remain in open-coast areas do not have these advantages, and could experience low survival. As an example of this, in 1988 Kramer (1990, 1991) collected most newly-settled halibut juveniles in open-coast areas, whereas bays contained larger sized juveniles; Kramer suggested that individuals that settled on the open coast eventually moved into bays or died. However, Kramer (1991) did not find a significant difference in growth rates of smaller juveniles ($\leq$40 mm standard length) from bay versus coastal locations.

The El Niño years of 1982 and 1983 may be an example of warm ocean temperatures enhancing juvenile halibut survival, both in open-coast areas and during normally colder seasons. Higher densities of juvenile halibut were collected in bays in 1983 (Allen 1988). Additionally, strong fishery catches of halibut 1982 and 1983 year-classes have been reported (Miller 1990, Pattison and McAllister 1990).

The mechanism of larval or juvenile halibut entry into bays, and the stage at which entry occurs, are unknown. Kramer (1990) found newly-settled halibut almost exclusively in southern California bays in 1987, whereas in 1988 most settled in shallow open coast areas and then possibly moved into bays. English sole *Parophrys vetulus* have been reported to enter bays both during and after metamorphosis (Misitano 1976, Boehlert and Mundy 1987, Rogers et al. 1988). Plaice *Pleuronectes platessa* settle in deeper waters and move into shallow areas after metamorphosis (Lockwood 1974). For both English sole and plaice, tidal stream transport is an important migration mechanism (van der Veer and Bergman 1986, Boehlert and Mundy 1987). Other physical factors that have been suggested to mediate shoreward migration of larval and juvenile fishes are often associated with river discharge (salinity; olfactory cues) (Creutzberg 1961, Boehlert and Mundy 1987), and are thus not as applicable in drier southern California, where rainfall is only 25–40 cm/year (Petersen et al. 1986). Temperature differences between near and offshore areas might be an important cue (Boehlert and Mundy 1988, Miller 1988), although the ability of halibut larvae and young juveniles to seek preferred temperatures has not been demonstrated.

High inshore densities of juvenile halibut are likely a combination of passive larval transport to coastal areas, followed by active inshore movement of larvae or juveniles mediated by environmental stimuli. Shoreward transport of pelagic fish eggs and larvae to coastal nursery grounds has been demonstrated to enhance cohort survival (Nelson et al. 1976, Parrish et al. 1981). Onshore and offshore surface water transport in nearshore southern California areas is sporadic and associated with late-spring and summer downwelling and upwelling events (Winant 1980, Dorman and Palmer 1981). Another possible mechanism of onshore transport is surface slicks generated by tidally forced internal waves (Kingsford and Choat 1986, Shanks

1988). Additionally, halibut eggs and larvae may be transported parallel to the shore, since a narrow nearshore current with a generally southward surface flow often occurs within 10–20km of the coast (Tsuchiya 1980, Winant and Bratkovich 1981).

The passive transport of pelagic halibut larvae off southern California is thus influenced by a variety of currents and oceanographic conditions. Our results indicate that halibut larvae that encounter warmer waters during transport may settle much sooner than those remaining in colder waters (Fig. 3). Therefore, larvae carried by alongshore currents might eventually settle near the entrances of bays or estuaries due to warmer waters in these areas. Larvae transported offshore during upwelling events would experience lower temperatures (Dorman and Palmer 1981), resulting in delayed settlement and the possibility of eventual shoreward transport into shallow coastal or inshore nursery areas where warm temperatures could stimulate settlement.

The ability of pelagic larvae of many marine invertebrates to delay settlement until an appropriate habitat is available has been well documented (Scheltema 1974, Doyle 1975). Fish larvae have not commonly been demonstrated to have this ability, although Victor (1986) reported that bluehead wrasse *Thalassoma bifasciatum* can extend the duration of the planktonic larval period after attaining settlement size by reducing growth rate. We found that halibut larvae at 16°C took about a week longer to 50% settlement than larvae reared initially at 16°C and then exposed to 20°C when 1 month old; one individual at 16°C was pelagic 12 days after all larvae had settled at 20°C (Fig. 3). Although the observed longer period to settlement at 16°C vs. 20°C was to some degree a direct growth response to temperature, halibut larvae in colder waters may additionally be capable of delaying settlement for a limited period until encountering the appropriate cue, higher temperatures. This trait would enhance larval halibut survival by increasing the likelihood of settlement in warmer inshore areas.

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Estimation of Southern Bluefin Tuna *Thunnus maccoyii* Growth Parameters from Tagging Data, using von Bertalanffy Models Incorporating Individual Variation

John Hampton

CSIRO Division of Fisheries, Marine Laboratories
GPO Box 1538, Hobart, Tasmania 7001, Australia
Present address: South Pacific Commission, BP D5, Noumea Cedex, New Caledonia

Abstract. – Von Bertalanffy growth models appropriate for fitting to length-increment data by maximum likelihood are described. Models incorporating variation in growth among individuals, release-length-measurement error, and model error are developed and fit to southern bluefin tuna *Thunnus maccoyii* tag-return data. On the basis of likelihood ratio tests, a model in which individual variation in growth is represented by variation in L_∞ and which explicitly incorporates model error is selected as the most appropriate model for these data. The parameter estimates obtained were $\mu_{L_\infty} = 186.9\,cm$, $\sigma_{L_\infty}^2 = 218.8\,cm^2$, $K = 0.1401$/year, and $\sigma_e^2 = 15.25\,cm^2$. Analyses of simulated data suggest that biased estimates of growth parameters can result if model error is not explicitly included in von Bertalanffy models incorporating individual variation in growth.

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Knowledge of the growth of a fish and, in particular, a mathematical description of the increase in length or weight with time, is important for understanding its population and fishery dynamics. Also, fish growth has been used directly or indirectly to calculate catch age composition (Hayashi 1974, Baglin 1977, Kume 1978, Skillman and Shingu 1980, Majkowski and Hampton 1983), mortalities (Beverton and Holt 1957, Pauly 1987) and yield-per-recruit (Beverton and Holt 1957, Ricker 1975) and to make inter- and intra-population comparisons (Brousseau 1979, Goldspink 1979, Kohlhorst et al.1980, Francis 1981).

Techniques for studying fish growth in length fall into three categories: (i) Direct measurements of age (such as those obtained by counting periodic protein and calcium depositions in scales, otoliths, vertebrae, fin rays, or some other hard tissue) and length; (ii) analysis of time series of length-frequency data (sometimes called modal progression analysis); and (iii) analysis of length-increment and time-at-liberty data from a mark-recapture experiment. In each case, a growth model is usually fit to the data. Various models have been proposed for fitting to these types of data (e.g., Brody 1927 and 1945, Ford 1933, Walford 1946, Richards 1959, Knight 1969), but by far the most used model in fisheries research is that of von Bertalanffy (1938). This model, originally formulated on physiological considerations, has three parameters that have the biological interpretations of average maximum length (L_∞), the average rate at which L_∞ is approached (K), and the theoretical average time at which length would be zero if growth had always occurred according to the model (t_0).

The study of growth by direct measurements of age (reviewed by Bagenal 1974, Brothers 1979, Beamish 1981, Prince and Pulos 1983) and length is not possible for many species. In particular, good estimates of the ages of older fish are frequently hard to come by. This was the case for Yukinawa's (1970) study of southern bluefin tuna *Thunnus maccoyii* age and growth from presumed annual rings on scales. He examined the scales of 2240 fish within the length range of 38–184 cm, but was able to age only about 15% of fish larger than 120 cm, and none of those larger than 153 cm. Similarly, Thorogood (1986) was unable to age significant numbers of large southern bluefin from examinations of their otoliths.

A major aspect of length-frequency analysis is the identification of age classes in the data. To do this, Harding (1949) and Cassie (1954) used probability paper, and Tanaka (1956) fit parabolas to the logarithms of

observed length-frequencies. More recently, digital computers have been used, and the distribution of length-at-age has been assumed to be normal or log-normal (Hasselblad 1966, Kumar and Adams 1977, Macdonald 1969 and 1975, Macdonald and Pitcher 1979, Schnute and Fournier 1980, Fournier and Breen 1983). Pauly's method (Pauly 1987) of fitting growth curves to observed peaks in a time series of length-frequency data, commonly known as ELEFAN I, has received some recent attention, but it suffers from the assumption that length-at-age does not vary (Hampton and Majkowski 1987).

Some attempts have been made to study the growth of southern bluefin, using length-frequency data. Serventy (1956) plotted the progressions of length-frequency means and modes of juvenile age classes caught in Australian coastal waters, but did not attempt to quantify the results as a growth equation. Robins (1963) made the first attempt to quantify growth, obtaining a Walford growth transformation from an analysis of length-frequency modes of juvenile fish. Hearn (1986) identified a seasonal component to growth from analyses of similar data. Recently, promising results have been obtained with the application of MULTIFAN, a likelihood-based method for estimating von Bertalanffy growth parameters from length-frequency data, to southern bluefin tuna data (Fournier et al. 1990).

Length-increment and time-at-liberty data from a tagging experiment provide direct measurements of the growth of individual fish as long as the tag or the tagging procedure does not have a significant effect on growth. Using a von Bertalanffy model and a fitting procedure such as that proposed by Fabens (1965), estimates of L_∞ and K can be obtained, but without additional assumptions no estimate of t_0 is available.

Murphy (1977) analyzed the release and recapture data from 2578 tagged southern bluefin and derived estimates of L_∞ and K that he considered to be more reliable than those previously derived by other workers. Kirkwood (1983) obtained similar estimates from a smaller data set (n 794), excluding fish that had been at liberty for less than 250 days. In addition, he incorporated age-at-length observations from length-frequency modes to the estimation procedure to obtain an estimate of t_0.

None of the studies of southern bluefin growth, and indeed few studies of fish growth in general, take explicit account of variation in growth among individuals by the incorporation of parameters describing such variation into the model. Krause et al. (1967) gave the first thorough treatment of individual variability in growth when deriving conditional probability densities for body weight-at-age of chickens. Sainsbury (1980) recognised the importance of individual variability in fishes showing von Bertalanffy growth, and derived equations appropriate for length-at-age and length-increment data if both L_∞ and K showed individual variation. He also showed that biased estimates of mean growth parameters could result if individual variability in K existed and was ignored. Kirkwood and Somers (1984) developed a simpler model for length-increment data in which only L_∞ was variable and applied it to two species of tiger prawn.

A problem with these models (as pointed out by Kirkwood and Somers 1984) is that all the observed "error" is attributed to individual variation in L_∞ and/or K. It is, of course, reasonable to expect that there will also be error due to some animals not growing exactly according to the von Bertalanffy model, a so-called model error. For standard growth models not incorporating individual variability, all residual error is assumed to be model error. It is also reasonable to expect that, in the case of length-increment data, the initial or release length cannot always be measured exactly and therefore will be an additional source of error.

In this paper, southern bluefin tuna tag-return data are analysed using three existing models, all of which are based on the von Bertalanffy model: the standard model, using the fitting procedure described by Fabens (1965), model (2) of Kirkwood and Somers (1984), and the Sainsbury (1980) model. In addition, models based on the latter two that incorporate model error and release-length-measurement error are derived and applied. The properties and assumptions of each of the models are investigated using computer simulation techniques.

Methods

Tagging methods and data

The primary method used to catch fish for tagging was commercial pole-and-line, using either live or dead bait, although on some occasions trolling was also used. Prior to release, the fork lengths of most fish selected for tagging were measured to the nearest centimeter on a measuring board. While the fish were restrained on the measuring board, one or two numbered tuna tags, each consisting of a molded plastic barbed head with a tubular plastic streamer glued to it (Williams 1982), were inserted forward into the musculature at an angle of about 45°, 1–2cm below the posterior insertion of the second dorsal fin. For double-tagged fish, one tag was inserted on each side of the second dorsal fin. Ideally, the tag barb was anchored behind the second dorsal fin ray supports (pterygiophores).

The primary data used in this study consist of returns of southern bluefin tagged between 1962 and 1978 that were measured to the nearest centimeter at release, were thought to have reliable dates of release and

recapture, and were at liberty for at least 250 days. These criteria were satisfied by 1800 returns. The last criterion was applied to eliminate the possible effect that the tagging operation might have on length growth and to minimize the biasing effect that seasonal fluctuations in growth, if present, might have on parameter estimation.

Most fish were 50–80 cm long when tagged, with the smallest 38 cm and the largest 104 cm. The range of recapture lengths was 51–185 cm, with most being in the range 60–100 cm. The times at liberty for the primary data set range from 250 days (the minimum allowed) to approximately 11 years.

Parameter estimation

Model 1: Standard von Bertalanffy model The form of the von Bertalanffy growth model appropriate for fitting to tag-return data (indexed by i) is, as described by Fabens (1965),

$$\delta l_i = (L_\infty - l_i)(1 - e^{-Kt_i}) + e_i \qquad (1)$$

where δl_i is the length increment, l_i is the release length, t_i is the time at liberty, and e_i is a model error term (or residual), all for the ith observation. The error term e_i is assumed to be a normally-distributed random variable with an expected value of zero and variance σ_e^2. Thus, for given l_i and t_i, δl_i is a normally-distributed random variable with an expected value of $(L_\infty - l_i)(1 - e^{-Kt_i})$ and a variance of σ_e^2. Estimates of L_∞, K, and σ_e^2 can be obtained by nonlinear ordinary least squares (as in Kirkwood and Somers 1984) or by maximum likelihood (Kimura 1980). In the case of model 1, either technique can be applied, since the variance of δl_i is assumed to be constant with increasing t_i. However, in the models that incorporate individual variability (see below), the variance of δl_i increases with increasing t_i. This would require the use of weighted least-squares if this approach was followed. Since the weights would depend on the estimated K, an iterative procedure would be necessary to obtain the appropriate estimates. Therefore, the maximum-likelihood method, which is far more straightforward, is used to obtain parameter estimates for this and the models that follow.

For n observations of δl_i and t_i (i = 1 to n), the likelihood function is

$$L = \prod_{i=1}^{n} (2\pi\sigma_e^2)^{-\frac{1}{2}} \exp\left[-\frac{[\delta l_i - E(\delta l_i)]^2}{2\sigma_e^2} \right],$$

and estimates of L_∞, K, and σ_e^2 are found by minimizing

$$LL = -\ln L = \frac{n}{2} \ln (2\pi\sigma_e^2) + \frac{\sum_{i=1}^{n} [\delta l_i - E(\delta l_i)]^2}{2\sigma_e^2}.$$

This was accomplished for all the models described in this paper, using the minimization subroutine MINIM (programmed by D.E. Shaw, CSIRO Div. Math. Stat., P.O. Box 218, Lindfield 2070, Aust.), which uses the method of Nelder and Mead (1965). Equivalent subroutines are available in several commercially-available software packages.

Model 2: Kirkwood and Somers model Kirkwood and Somers (1984) described a model which allowed for individual variation in growth through an individually variable L_∞. Specifically, L_∞ was assumed to be normally distributed with mean μ_{L_∞} and variance $\sigma_{L_\infty}^2$. For given l_i and t_i, δl_i is a normally-distributed random variable whose expected value is given by

$$E(\delta l_i) = (\mu_{L_\infty} - l_i)(1 - e^{-Kt_i}) \qquad (2)$$

and variance by

$$\text{var}(\delta l_i) = \sigma_{L_\infty}^2 (1 - e^{-Kt_i})^2.$$

The negative log-likelihood function now becomes

$$LL = \sum_{i=1}^{n} \frac{\ln [2\pi \text{ var}(\delta l_i)]}{2} + \frac{[\delta l_i - E(\delta l_i)]^2}{2 \text{ var}(\delta l_i)} \qquad (3)$$

from which maximum likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}^2$, and K may be obtained.

Model 3: Kirkwood and Somers model with model error Let us now assume that the variance of δl_i is comprised of components due to both the individual variation in L_∞ and to a normally-distributed model error, e_i, having a mean of zero and variance σ_e^2. In this case, $E(\delta l_i)$ is unchanged from Equation (2) and the variance of δl_i is given by

$$\text{var}(\delta l_i) = \sigma_{L_\infty}^2 (1 - e^{-Kt_i})^2 + \sigma_e^2. \qquad (4)$$

Maximum-likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}^2$, K, and σ_e^2 can again be obtained by substituting the right sides of Equations (2) and (4) into Equation (3).

Model 4: Kirkwood and Somers model with model error and release-length-measurement error Because the tagging operation involves the handling of powerful, often violently struggling fish, it is quite reasonable to expect that release length will be measured with error. If possible, this error should be independently estimated and included in the growth model. On the other hand, measurement of a dead fish at recapture should not involve a significant error if competently carried out. In this study, recapture lengths are assumed to be measured without error.

If growth is assumed to be negligible, a comparison of lengths-at-release and lengths-at-recapture (l_2) for animals at liberty for a very short time should provide a good estimate of release-length-measurement error. Such a comparison was made for 251 tag returns in which the release length was 50 cm or more (see Residuals Analysis section) and the period at liberty was 10 days or less. For this data set, the mean measurement error $\mu_m = (\Sigma\{l_2 - l_1\}/251)$ was 0.4861 cm with a variance, σ_m^2, of 5.2428 cm^2. At least some of this μ_m might be attributed to growth, since the average growth increment over a 10-day period is approximately 0.5 cm. In this paper, μ_m is assumed to be zero.

Because δl_i now depends on another random variable (l_i), it is convenient to assume that the length-at-recapture is a normally-distributed random variable. Equation (1) can be modified to describe the i th recapture length as

$$l_{2i} = [\mu_{L_\infty} - (l_i + \varepsilon_i)]\,[1 - e^{-Kt_i}] + l_i + \varepsilon_i + e_i, \qquad (5)$$

where ε_i is the normally-distributed release-length-measurement error. The expected value of l_{2i} is given by

$$E(l_{2i}) = [\mu_{L_\infty} - E(l_i)]\,[1 - e^{-Kt_i}] + E(l_i),$$

where $E(l_i)$ is equal to $l_i + \mu_m$. Collecting terms in ε_i, Equation (5) is rewritten as

$$l_{2i} = [\mu_{L_\infty} - l_i]\,[1 - e^{-Kt_i}] + l_i + e^{-Kt_i}\,\varepsilon_i + e_i.$$

The variance of l_{2i} is then given by

$$\text{var}\,(l_{2i}) = \sigma_{L_\infty}{}^2\,(1 - e^{-Kt_i})^2 + \sigma_e{}^2 + \sigma_m{}^2\,e^{-2Kt_i}.$$

Given estimates of μ_m and $\sigma_m{}^2$, maximum-likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}{}^2$, K, and $\sigma_e{}^2$ can be obtained as before.

Model 5: Sainsbury model Sainsbury (1977, 1980) described a model that recognised individual variation in K, as well as in L_∞. He assumed that both were independent random variables, with K following a gamma distribution and L_∞ being normally distributed. He also assumed that, as an approximation, δl_i is normally distributed for given l_i and t_i, pointing out that this should involve little error if L_∞ is normally distributed (Sainsbury 1977). With μ_K and $\sigma_K{}^2$ denoting the mean and variance, respectively, of K, the relevant equations are

$$E(\delta l_i) = [\mu_{L_\infty} - l_i]\left[1 - \left[1 + \frac{\sigma_K{}^2\,t_i}{\mu_K}\right]^{-\frac{\mu_K{}^2}{\sigma_K{}^2}}\right]$$

and

$$\text{var}\,(\delta l_i) = C_1\,\sigma_{L_\infty}{}^2 + C_2\,(\mu_{L_\infty} - l_i)^2, \qquad (6)$$

where

$$C_1 = 1 - 2\left[1 + \frac{\sigma_K{}^2\,t_i}{\mu_K}\right]^{-\frac{\mu_K{}^2}{\sigma_K{}^2}} + \left[1 + \frac{2\sigma_K{}^2\,t_i}{\mu_K}\right]^{-\frac{\mu_K{}^2}{\sigma_K{}^2}}$$

and

$$C_2 = \left[1 + \frac{2\sigma_K{}^2\,t_i}{\mu_K}\right]^{\frac{\mu_K{}^2}{\sigma_K{}^2}} - \left[1 + \frac{\sigma_K{}^2\,t_i}{\mu_K}\right]^{-\frac{2\mu_K{}^2}{\sigma_K{}^2}}$$

Maximum-likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}{}^2$, μ_K, and $\sigma_K{}^2$ can be obtained as shown earlier.

Model 6: Sainsbury model with model error As shown in model 3, a model error can be included simply by adding the model error variance term to Equation (6) giving

$$\text{var}\,(\delta l_i) = C_1\,\sigma_{L_\infty}{}^2 + C_2\,(\mu_{L_\infty} - l_i)^2 + \sigma_e{}^2.$$

Solution by maximum likelihood now requires that a fifth parameter, $\sigma_e{}^2$, be estimated from the data.

Model 7: Sainsbury model with model error and release-length-measurement error Using logic similar to that developed in model 4, length-at-recapture is now considered as the random variable and assumed

to be normally distributed, with

$$E(l_{2i}) = [\mu_{L_\infty} - E(l_i)]\left[1 - \left[1 + \frac{\sigma_K^2 t_i}{\mu_K}\right]^{-\frac{\mu_K^2}{\sigma_K^2}}\right] + E(l_i) \quad (7)$$

and

$$\text{var}(l_{2i}) = C_1 \sigma_{L_\infty}^2 + C_2 [\mu_{L_\infty} - E(l_i)]^2 + \sigma_e^2 + \sigma_m^2 E(e^{-2Kt_i}), \quad (8)$$

where

$$E(e^{-2Kt_i}) = \left[1 + \frac{2\sigma_K^2 t_i}{\mu_K}\right]^{-\frac{\mu_K^2}{\sigma_K^2}}$$

Given the estimate of σ_m^2 derived for model 4, maximum-likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}^2$, μ_K, σ_K^2, and σ_e^2 can be obtained as before.

Estimation of t_0 An estimate of t_0 is required for many applications of the von Bertalanffy model, but this parameter cannot be estimated from tag-return data alone. To estimate t_0, one or more observations of age-at-length are required. Kirkwood (1983) described a maximum-likelihood method for determining t_0, along with L_∞ and K, if supplementary age-length data are available in addition to tag-return data. Such data can easily be accommodated in the models described above. Consider the case where n1 tag returns (δl_i and δt_i) and n2 age-length observations (l_j and t_j) are available. We now have two random variables, δl_i and l_j, which have normal probability density functions conditioned on l_i (release length) and δt_i, and t_j, respectively. Their expected values, for example in the case of model 3, are given by

$$E(\delta l_i) = (\mu_{L_\infty} - l_i)(1 - e^{-K\delta t_i})$$

$$E(l_j) = \mu_{L_\infty}(1 - e^{-K(t_j - t_0)})$$

and their variances by

$$\text{var}(\delta l_i) = \sigma_{L_\infty}^2 (1 - e^{-K\delta t_i})^2 + \sigma_{e1}^2$$

$$\text{var}(l_j) = \sigma_{L_\infty}^2 (1 - e^{-K(t_j - t_0)})^2 + \sigma_{e2}^2$$

where σ_{e1}^2 and σ_{e2}^2 are independent model error variances. Maximum-likelihood estimates of μ_{L_∞}, $\sigma_{L_\infty}^2$, K, t_0, σ_{e1}^2, and σ_{e2}^2 could, in theory, be found by minimizing

$$LL = \sum_{i=1}^{n1} \frac{\ln[2\pi \text{ var}(\delta l_i)]}{2} + \frac{[\delta l_i - E(\delta l_i)]^2}{2 \text{ var}(\delta l_i)} + \sum_{j=1}^{n2} \frac{\ln[2\pi \text{ var}(l_j)]}{2} + \frac{[l_j - E(l_j)]^2}{2 \text{ var}(l_j)}. \quad (9)$$

However, the estimation of six parameters (or seven in the case of models 6 and 7) may prove unrealistic in many cases. In order to obtain an approximate estimate of t_0, I have employed a simpler procedure. It involves fixing the growth parameters estimated from tag-return data and estimating t_0 by minimizing only the second summation in Equation (9), using the same approximate age-length data as Kirkwood (1983). I did not attempt to estimate simultaneously all parameters using the combined length-increment and age-length data because of the approximate nature of the latter data.

Model selection

An important part of this study was to select the most appropriate growth model for use in southern bluefin tuna stock assessments. Although L provides a means of comparing the goodness of fit of the various growth models with the tagging data, it is not immediately clear whether the more complex models result in a statistically-significant improvement in fit to the data. Likelihood ratio tests (Mendenhall and Scheaffer 1973, Kendall and Stuart 1979, Kimura 1980) can be used to address this question.

Likelihood ratio tests Let λ be defined by

$$\lambda = \frac{L(\phi_0)}{L(\phi_a)},$$

where $L(\phi_0)$ and $L(\phi_a)$ are the maximum-likelihood function values under the null hypothesis (the simple model is correct) and the alternative hypothesis (the more complex model is correct), ϕ_0 is the set of maximum-likelihood estimates of r parameters under the null hypothesis, and ϕ_a is the set of maximum-likelihood estimates of r + s parameters under the alternative hypothesis. Under certain regularity assump-

tions that hold under most circumstances for large sample sizes (Mendenhall and Scheaffer 1973), $-2\log_e\lambda$ behaves as a χ^2 random variable with s degrees of freedom. Therefore $-2\log_e\lambda$ may be compared with a critical χ^2 value (pertaining to a suitable rejection region) and the null hypothesis either accepted or rejected. For example, a value of $-2\log_e\lambda$ of more than 3.84 would lead to rejection of the simple model in favor of a model with one extra parameter (df 1) with a rejection region (significance level) of 0.05 on the χ^2 distribution.

Simulations

Assessment of model performance One hundred simulated data sets were produced and analysed by the models described above. The simulated data sets were produced by simulating values of δl_i (for each of the 1736 observations comprising the edited data set), using the following equation,

$$\delta l_i = [L_{\infty i} - (l_i + \varepsilon_i)]\,[1 - e^{-K_i t_i}] + e_i.$$

$L_{\infty i}$ and e_i were sampled from normal distributions, and K_i from a gamma distribution defined by the model 7 maximum-likelihood estimates of their respective μ's and σ^2's. The release-length-measurement error, ε_i, was sampled from a normal distribution with a mean of 0 and a variance of 5.2428 cm^2. Subroutine GGNML of the International Mathematical and Statistical Library (IMSL) was used to generate random normal deviates. IMSL subroutine GGAMR was used to generate gamma deviates. Actual values of l_i and t_i from the edited data set were used.

A second set of simulations was undertaken, assuming $L_{\infty i}$ and K_i to be correlated with a correlation coefficient of 0.80. Correlated normal deviates were generated, using IMSL subroutine GGNSM. This was done to test the sensitivity of the models to the assumption of independence of $L_{\infty i}$ and K_i observations. In this set of simulations, K was assumed, for simplicity, to be normally distributed, rather than gamma distributed. With the values of μ_K and σ_K^2 encountered in this study, the gamma and normal distributions are virtually indistinguishable, and therefore the normal approximation should result in little or no error. This was confirmed in a small number of simulations where analyses of simulated data, produced using normally-distributed K_i values (uncorrelated with $L_{\infty i}$), gave results virtually identical to simulations where K_i was gamma distributed.

Analysis of the 100 simulated data sets by each of the models described above provided 100 sets of parameter estimates for each. The means and standard errors of these estimates were calculated to (i) derive approximate confidence intervals for the maximum-likelihood estimates produced by the models and (ii) compare model performance, i.e., their ability to estimate known parameter values.

Testing the assumption of normally-distributed l_{2i} The assumption that, given l_i and t_i, the random variable δl_i (or l_{2i} in the case of models 4 and 7) is normally distributed, is central to all the models described. This assumption is most questionable for model 7, where K variability and release-length-measurement error could have unpredictable effects on the distribution of l_{2i}. This assumption was tested for 30 combinations of l and t by generating 5000 values of l_{2i} for each combination, using the following equation.

$$l_{2i} = [L_{\infty i} - (l + \varepsilon_i)]\,[1 - e^{-K_i t}] + l + \varepsilon_i + e_i.$$

A χ^2 goodness-of-fit test (IMSL subroutine GPNOR) with 50 equiprobable categories was then applied to identify possible departures from a normal distribution with mean and variance given by Equations (7) and (8), respectively. Values of l of 50, 60, 70, 80, 90, and 100 cm were combined with values of t of 2, 4, 6, 8, and 10 years to produce the 30 combinations.

Results

Residuals analysis

Using model 1, an analysis of residuals was carried out on the primary data set. An initial fit of model 1 to the 1800 observations yielded estimates of L_∞, K, and σ_e^2 of 195.614 cm, 0.131914/year, and 24.8193 cm^2, respectively. Standardized residuals ($R_i = e_i/\sigma_e$) were calculated and plotted against t_i (Fig. 1) and against l_i (Fig. 2). Examination of Figure 1 reveals an even distribution of standardized residuals about zero and no obvious relationship with time at liberty. However, Figure 2 suggests that the fit model may not be appropriate over the entire range of release lengths observed. For release lengths less than 50 cm, there are 54 positive residuals but only 8 negative residuals, indicating that observed growth was faster than the model would predict for these smaller fish. For release lengths of 50 cm and larger, the pattern of residuals is unremarkable. On this basis, observations with release lengths smaller than 50 cm were excluded from further analyses.

A refit of model 1 to the amended data set (1738 observations) provided estimates of L_∞, K, and σ_e^2 of 200.120 cm, 0.125836/year, and 23.6157 cm^2, respectively. Using these parameter estimates, standardized

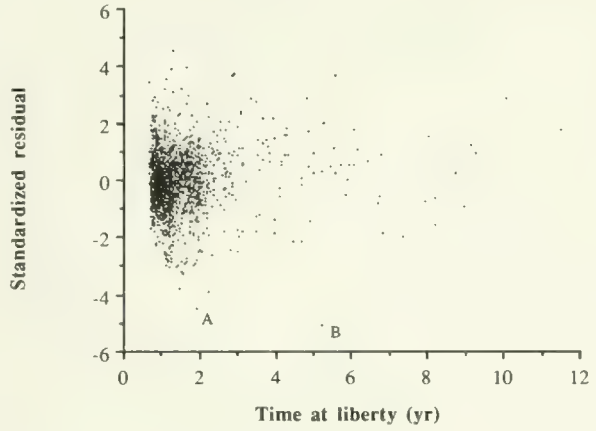

Figure 1

Plot of standardized residuals against time-at-liberty following an initial fit of model 1 to the primary data set (n 1800). The parameter estimates used were $L_\infty = 195.614$ cm, K = 0.131914/year, and $\sigma_e^2 = 24.8193\,cm^2$. The observations labeled A and B are those identified as outliers.

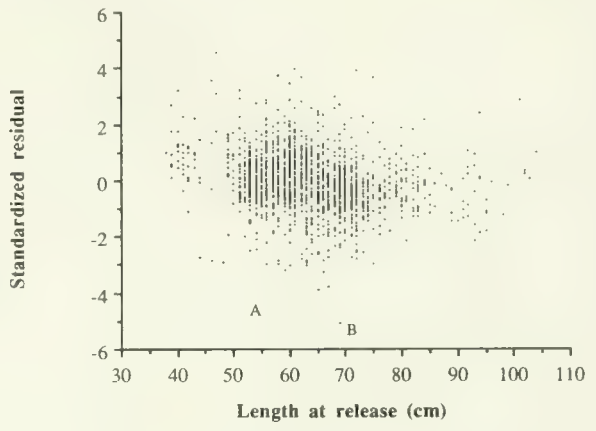

Figure 2

Plot of standardized residuals against release length following an initial fit of model 1 to the primary data set (n 1800). The parameter estimates used were $L_\infty = 195.614$ cm, K = 0.131914/year, and $\sigma_e^2 = 24.8193\,cm^2$. The observations labeled A and B are those identified as outliers.

residuals were recalculated and checked for outliers. Models 2–7 incorporate individual variability in growth parameters, necessitating the use of a quite severe criterion in the definition of an outlier. An observation was classified as an outlier only if the absolute value of its standardized residual was greater than 4.4172. Under the assumptions of model 1, only one in 2000 observations would exceed this value due to chance alone. Two observations were classified as outliers on this basis and rejected from further analyses. These observations are indicated in Figures 1 and 2. The final data set to which all models were fitted consisted of 1,736 observations.

Parameter estimates

Parameter estimates for the seven models fitted to the final data set are given in Table 1. The estimates differ substantially among some models, which is not surprising since they are based on rather different assump-

Table 1

Southern bluefin tuna growth parameter estimates derived for the seven models described.

Model no.	Model description	μ_{L_∞} (cm)	μ_K/yr	$\sigma_{L_\infty}^2$ (cm^2)	σ_K^2/yr^2	σ_e^2 (cm^2)	t_0 (yr)	LL
1	Fabens	201.1	0.1251			22.96	−0.6884	5183.66
2	Kirkwood and Somers	157.2	0.1892	555.8			−0.2506	5224.31
3	Kirkwood and Somers, with model error	186.9	0.1401	218.8		15.25	−0.5437	5150.86
4	Kirkwood and Somers, with model error and release-length error	186.2	0.1409	238.2		10.92	−0.5396	5151.06
5	Sainsbury	175.2	0.1563	100.7	0.1665E-02		−0.4660	5207.39
6	Sainsbury, with model error	188.3	0.1384	177.8	0.8824E-04	15.00	−0.5620	5150.80
7	Sainsbury, with model error and release-length error	188.0	0.1387	193.0	0.1014E-03	10.56	−0.5601	5150.97

Table 2

Estimates of mean and standard deviation of length-at-age (in cm), based on the parameter estimates for models 1 to 7.

	Model 1		Model 2		Model 3		Model 4		Model 5		Model 6		Model 7	
Age	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	38.3	4.8	33.1	5.0	36.3	4.8	36.6	4.5	35.6	8.5	36.6	5.2	36.6	4.9
2	57.4	4.8	54.5	8.2	56.0	5.9	56.0	5.7	55.4	12.2	56.2	6.4	56.1	6.3
3	74.3	4.8	72.2	10.8	73.1	7.0	73.1	6.9	72.3	14.7	73.2	7.5	73.2	7.5
4	89.2	4.8	86.9	13.0	88.0	8.0	88.0	8.0	86.6	16.3	88.1	8.5	88.0	8.6
5	102.4	4.8	99.0	14.8	100.9	8.9	100.9	9.0	98.8	17.3	101.0	9.3	100.9	9.5
6	114.0	4.8	109.0	16.3	112.2	9.7	112.1	9.9	109.3	17.7	112.2	10.0	112.1	10.2
7	124.2	4.8	117.3	17.6	121.9	10.4	121.8	10.6	118.2	17.8	122.0	10.6	121.9	10.8
8	133.3	4.8	124.2	18.6	130.4	11.1	130.3	11.3	125.8	17.6	130.5	11.0	130.4	11.3
9	141.2	4.8	129.9	19.5	137.8	11.6	137.6	11.9	132.4	17.3	138.0	11.4	137.8	11.7
10	148.3	4.8	134.6	20.2	144.2	12.1	144.0	12.4	138.0	16.8	144.4	11.8	144.3	12.0
11	154.5	4.8	138.5	20.8	149.8	12.5	149.6	12.8	142.9	16.3	150.1	12.0	149.9	12.4
12	160.0	4.8	141.7	21.2	154.7	12.9	154.4	13.2	147.1	15.8	155.0	12.3	154.8	12.6
13	164.8	4.8	144.4	21.6	158.9	13.2	158.6	13.5	150.7	15.2	159.2	12.5	159.1	12.8
14	169.1	4.8	146.6	22.0	162.5	13.5	162.2	13.8	153.8	14.7	163.0	12.6	162.8	13.0
15	172.9	4.8	148.4	22.3	165.7	13.7	165.3	14.1	156.5	14.2	166.2	12.8	166.0	13.1
16	176.2	4.8	149.9	22.5	168.5	13.9	168.1	14.3	158.8	13.7	169.0	12.9	168.8	13.3
17	179.1	4.8	151.2	22.7	170.9	14.1	170.5	14.5	160.9	13.3	171.5	13.0	171.3	13.4
18	181.7	4.8	152.2	22.8	173.0	14.3	172.5	14.7	162.6	12.8	173.6	13.1	173.4	13.5
19	184.0	4.8	153.1	23.0	174.8	14.4	174.3	14.8	164.2	12.5	175.5	13.2	175.3	13.6
20	186.0	4.8	153.8	23.1	176.4	14.5	175.9	14.9	165.5	12.1	177.2	13.3	176.9	13.7

tions. The effect of these differences on the mean and standard deviation of length-at-age is shown in Table 2. Despite the differences in parameter estimates, mean length-at-age is virtually identical for all models up to age 7. This allows the calculation of an approximate age-at-release for each observation that should contain little error and that is essentially independent of which set of parameter estimates is used to convert the release length to age. With this information, a presumed age-at-recapture incorporating individual variation can be calculated by adding the presumed age-at-release to the observed period at liberty. A plot of presumed age-at-recapture (calculated using the model 3 parameter estimates) against recapture length is shown in Figure 3.

Figure 3

Plot of recapture length against presumed age-at-recapture for tag returns comprising the final data set (n 1736).

Model 1 produced the highest estimate of μ_{L_∞} and the lowest estimate of μ_K. The probable explanation for this is that the estimates are biased by the three observations with the greatest recapture lengths (Fig. 3). Because there is no individual variation in this model, the estimate of L_∞ is forced upward to compensate for these influential observations. In model 2, such observations can be accommodated by individual variation in L_∞; thus the estimate of μ_{L_∞} falls by more than 20% and the estimate of μ_K rises by more than 50%. When a model error term is added (model 3), the differences in relation to model 1 are less dramatic. The addition of release-length-measurement error (model 4) has little effect on the model-3 estimates, with the exception of σ_e^2, which is somewhat lower in model 4. Similar effects of adding model error and release-length-measurement error can be seen in comparisons of the parameter estimates for models 5, 6, and 7.

The estimates of $\sigma_{L_\infty}^2$ are substantially higher for models that assume constant K (models 2, 3, and 4) than for those that assume individual variability in K

Table 3
Values of the 97.5 percentile of the L_∞ distributions derived for models 2–7. These values may be compared with an observed maximum size in the catch of 225 cm.

Model no.	97.5 percentile of the L_∞ distribution (cm)
2	203.4
3	216.0
4	216.5
5	194.8
6	214.4
7	215.2

(models 5, 6, and 7). An approximate consistency test for derived L_∞ distributions is to compare an upper percentile (e.g., 97.5) of the distribution with the observed maximum size in a large sample of the catch (Kirkwood and Somers 1984). The largest southern bluefin ever measured by Japanese researchers during many years of length-frequency sampling is 225 cm (Yukinawa 1970, Shingu 1978). This may be compared with the derived 97.5 percentile of the L_∞ distributions for models 2–7 (Table 3). While by no means a definitive test, the comparisons suggest that the L_∞ distributions derived for models 3, 4, 6, and 7 (models that include model error) are more consistent with the observed maximum length than the distributions derived for models 2 and 5 (models that do not include model error).

The estimate of σ_K^2 for model 5 fell substantially with the addition of model error (models 6 and 7). The value of σ_K^2 for model 7 represents a coefficient of variation of approximately 7%. It should be pointed out here that the log-likelihood surface was very flat with respect to both $\sigma_{L_\infty}^2$ and σ_K^2, i.e., relatively large changes in either parameter resulted in only very small changes in LL. This matter is explored further using simulation techniques.

Model selection

The minimum negative log-likelihood function values given in Table 1 are indicators of the goodness of fit of the models to the data. Model 2 (3 parameters) provided a substantially poorer fit to the data than model 1 (3 parameters) and therefore need not be tested. Also, the inclusion of release-length-measurement error resulted in slightly worse fits to the data, eliminating models 4 and 7 from further consideration. The only likelihood ratio tests that are required are: (1) the null hypothesis (H_0) that model 1 is the correct model against the alternative that model 3 (4 parameters) is correct; (2) the H_0 that model 1 is the correct model against the alternative that model 6 (5 parameters) is correct; and (3) the H_0 that model 3 is the correct model against the alternative that model 6 is correct. H_0 was rejected for both tests (1) and (2) ($P<0.001$), indicating that the more complex models 3 and 6 provide significantly better fits to the data than model 1. For test (3), H_0 was accepted ($P>0.05$), suggesting that the additional complexity of the extra parameter (σ_K^2) in model 6 did not result in a significantly improved fit over model 3. On this basis, model 3 was adopted as the most appropriate model for these data.

Simulations

Assessment of model performance The results of analyses of 100 simulated data sets, produced assuming independence of $L_{\infty i}$ and K_i, are given in Table 4. These suggest that all of the models, with the possible exception of model 2, provide unbiased estimates of μ_{L_∞} and μ_K. This is somewhat surprising in view of the wide range of estimates of these parameters obtained from analyzing real data with the same models (Table 1). In particular, one might have expected, on the basis of analyses of the real data, that models 2 and 5 would have given biased estimates of μ_{L_∞} and μ_K for the simulated data also. The estimates of these parameters obtained from the real data, using the above models, even lie outside the approximate 95% confidence bounds calculated from the simulated data. A possible explanation for this is that the simulated data do not contain all the growth-related features of the real data. Such unaccounted-for structure, if it affected the performance of the models differently, could produce such inconsistencies. This, in fact, was observed in the case of the apparently biased estimates given by model 1 for the real data.

While the simulations indicate that estimates of the mean parameters are relatively unbiased and precise, this is not the case for estimates of their variances. In particular, it is clear that reliable estimates of σ_K^2 cannot be obtained from this data set, since estimates from the simulated data ranged from practically zero to 25% (expressed as the coefficient of variation). This could be due in part to the loss of information on K-variability incurred because of the necessary exclusion from the analyses of fish at liberty for less than 250 days.

The mean values of $\sigma_{L_\infty}^2$ are reasonably consistent with the estimates obtained from the real data. The estimates from models 2, 3, and 4 are positively biased, while those from model 5 are negatively biased. The estimates from model 7 are unbiased, but have a coefficient of variation of 45%. The estimates of σ_e^2 are somewhat less than those obtained from the real data, except in the case of model 1.

Table 4

Results of analyzing 100 simulated data sets generated using model 7, assuming independence of L_∞ and K_i. The true parameter values (i.e., those input to the simulation model) were those estimated from the real data using model 7 (Table 1).

		Model						
Parameter		1	2	2	4	5	6	7
μ_{L_∞} (cm)	mean	189.5	179.9	189.1	190.7	188.1	189.1	189.0
	SE	5.8	5.0	5.0	9.2	5.7	5.9	4.8
	lower c.b.*	178.3	170.0	179.4	172.6	177.0	177.6	179.5
	upper c.b.	200.8	189.8	198.8	208.8	199.2	200.7	198.4
μ_K yr	mean	0.1372	0.1498	0.1376	0.1362	0.1400	0.1379	0.1378
	SE	0.0071	0.0074	0.0062	0.0093	0.0070	0.0074	0.0061
	lower c.b.	0.1233	0.1352	0.1256	0.1179	0.1263	0.1234	0.1259
	upper c.b.	0.1510	0.1644	0.1497	0.1544	0.1536	0.1525	0.1497
σ_L (cm)	mean		699.2	249.7	288.4	27.1	178.1	186.3
	SE		64.2	44.1	100.5	42.3	93.4	84.8
	lower c.b.		573.4	163.3	91.4	−55.8	−5.0	20.1
	upper c.b.		825.0	336.1	485.4	110.0	361.2	352.4
σ_K yr	mean					0.1176 E-2	0.1973 E-3	0.1839 E-3
	SE					0.1509 E-2	0.2503 E-3	0.1476 E-3
	lower c.b.					0.8806 E-3	−0.2932 E-3	−0.1054 E-3
	upper c.b.					0.1472 E-2	0.6879 E-3	0.4733 E-3
σ_ε^2 (cm^2)	mean	20.11		11.13	6.67		10.08	6.04
	SE	0.75		0.97	1.11		1.49	1.17
	lower c.b.	18.63		9.22	4.50		7.16	3.75
	upper c.b.	21.59		13.03	8.85		13.00	8.32

*95% confidence bound assuming variables to be normally distributed.

The results of the simulations in which $L_{\infty i}$ and K_i were assumed to be correlated are given in Table 5. These results are essentially identical to those in Table 4; therefore, the assumption of independence does not affect parameter estimation in this instance.

Testing the assumption of normally-distributed l_{2i}

Tests of normality of l_{2i} were performed for 30 combinations of l and t. For each of the combinations, the statistic G (χ^2 distributed with 49 degrees of freedom) and the probability, P, of wrongful rejection of the null hypothesis of normally-distributed l_{2i} were calculated (Table 6). In each case, P is greater than 0.10, and usually substantially so; therefore the null hypothesis is not rejected for any of the combinations of l and t.

Discussion

The estimation of von Bertalanffy growth parameters is one of the more frequently applied analyses in fisheries research. Despite this, the interpretation of the parameter estimates is often ill-founded. This is particularly so with L_∞, which is frequently given the interpretation of maximum possible length. This would be the case only if every fish grew exactly according to the derived model, i.e., there was no model error or individual variation in growth. In reality, the growth of all individual fish will not follow a single von Bertalanffy growth curve exactly; there will be variations among individuals resulting from exogenous (environmental) and endogenous (genetic) effects (Francis 1988). The correct interpretation of L_∞ estimated in the standard way is that it is the average maximum length that would be attained in the population represented by the data being analysed. Models have been proposed in this paper that take explicit account of model error and individual variation in growth, thereby eliminating the need for such interpretations.

Previous estimates of southern bluefin growth parameters have differed substantially (Table 7). The previous estimates of L_∞ obtained from tag-return data are somewhat smaller than the estimate derived using model 1 in this paper. This is possibly because

Table 5

Results of analyzing 100 simulated data sets generated using model 7, assuming correlated L_∞, and K_i pairs. The true parameter values (i.e., those input to the simulation model) were those estimated from the real data using model 7 (Table 1).

Parameter		Model 1	2	2	4	5	6	7
μ_{L_∞} (cm)	mean	188.2	178.5	187.6	187.3	186.3	187.1	184.6
	SE	6.6	4.9	5.0	5.1	5.6	6.4	7.8
	lower c.b.*	175.3	168.9	177.7	177.3	175.4	174.6	169.4
	upper c.b.	201.1	188.2	197.5	197.4	197.2	199.6	199.9
μ_K/yr	mean	0.1389	0.1517	0.1395	0.1398	0.1423	0.1404	0.1442
	SE	0.0083	0.0075	0.0065	0.0066	0.0072	0.0080	0.0111
	lower c.b.	0.1226	0.1370	0.1268	0.1269	0.1280	0.1248	0.1224
	upper c.b.	0.1553	0.1664	0.1521	0.1527	0.1563	0.1560	0.1661
$\sigma_{L_\infty}^2$ (cm^2)	mean		688.6	251.3	270.6	38.6	180.9	151.0
	SE		64.3	35.4	36.2	54.2	91.2	94.4
	lower c.b.		562.7	181.9	199.6	−67.6	2.2	−34.0
	upper c.b.		814.6	320.6	341.6	144.7	359.6	336.1
σ_K^2/yr^2	mean					0.1208 E-2	0.2105 E-3	0.4301 E-3
	SE					0.1608 E-3	0.2771 E-3	0.4383 E-3
	lower c.b.					0.8928 E-3	−0.3327 E-3	−0.4290 E-3
	upper c.b.					0.1523 E-2	0.7536 E-3	0.1289 E-2
σ_e^2 (cm^2)	mean	20.33		11.05	6.74		9.99	4.53
	SE	0.79		1.05	1.06		1.74	2.79
	lower c.b.	18.78		8.99	4.66		6.57	−0.95
	upper c.b.	21.88		13.12	8.82		13.41	10.00

*95% confidence bound assuming variables to be normally distributed.

Table 6

Values of the goodness-of-fit test statistic, G (χ^2 distributed with 49 degrees of freedom), and the probability, *P*, of wrongful rejection of the null hypothesis of normally-distributed recapture lengths. Each test consisted of 5000 recapture lengths generated for a specific combination of release length and time-at-liberty. For the purpose of calculating G statistics, the simulated recapture lengths were classified into 50 equiprobable categories.

Release length (cm)		Time-at-liberty (yr) 2	4	6	8	10
50	G	42.02	56.00	58.16	51.68	44.68
	P	0.75	0.22	0.17	0.37	0.65
60	G	57.54	50.86	52.38	38.74	46.84
	P	0.19	0.40	0.34	0.85	0.56
70	G	46.50	37.84	38.92	49.84	42.44
	P	0.58	0.88	0.85	0.44	0.73
80	G	56.68	45.62	60.92	40.42	48.58
	P	0.21	0.61	0.12	0.80	0.49
90	G	51.58	56.70	53.94	45.42	58.86
	P	0.37	0.21	0.29	0.62	0.16
100	G	54.96	45.70	46.70	31.94	43.78
	P	0.26	0.61	0.57	0.97	0.68

previous studies did not restrict the data to those observations where release length was at least 50 cm and time at liberty at least 250 days (except Kirkwood 1983 in the case of the latter restriction).

The estimates of L_∞ and K based on length-frequency data only (Shingu 1970, Hynd and Lucas 1974, Kirkwood 1983) and those based on scale (Yukinawa 1970) and otolith readings (Thorogood 1986) must be treated with caution because they were estimated from samples which consisted of no, or very few, larger fish (in the case of length-frequency data, modes are rarely visible beyond 100 cm). As discussed by Knight (1968), this almost inevitably leads to biased estimates of the growth parameters.

The analyses of both real and simulated data indicate that biased parameter estimates may result if model error is ignored. In addition, the incorporation of

Table 7
Southern bluefin tuna growth parameter estimates derived by other workers.

Source	Method	L_∞ (cm)	K/yr	t_0 (yr)	n
Shingu (1970) (data from Robins 1963)	Length-frequency	222.5	0.140	0.011	?
Shingu (1970)	Tag return	187.4	0.149	0.021	?
Yukinawa (1970)	Scales	219.7	0.135	0.040	1025
Hynd and Lucas (1974)	Length-frequency	220.0	0.150		?
Murphy (1977)	Tag return	180.8	0.146	−0.011	2578
Hearn (unpubl.)	Tag return	178.6	0.117	−0.010	629
Kirkwood (1983)	Tag return	185.3	0.155		794
	Tag return*	209.0	0.125		794
	Length-frequency	184.2	0.166	−0.036	77
	Length-frequency*	214.8	0.133	−0.095	77
	Tag return and length-frequency	184.4	0.157	−0.215	794+77
	Tag return and length-frequency*	207.6	0.128	−0.394	794+77
Thorogood (1986)	Otoliths	261.3	0.108	−0.157	~480

*Time-at-liberty and/or age assumed to be the dependent variable.

model error to both the Kirkwood and Somers model and the Sainsbury model resulted in significantly better fits to the data. This suggests that growth models that include individual variability should, if possible, include model error in the estimation procedure.

Release-length-measurement error did not prove to be a significant source of error in this case. However, its effect should, if possible, be tested in tag-recapture growth studies and, if significant, incorporated into the model as shown in this paper. This will be essential if negative length increments are included in the data set being analysed.

Sainsbury (1980) showed that an underestimate of mean K can result if substantial individual variability in K is present but ignored. There are a number of indications from southern bluefin data that the level of individual variability in K is not substantial. First, there is virtually no difference in estimates of μ_{L_∞} and μ_K between models 3 and 6 and between models 4 and 7. (The only difference in the models in each case is that both the latter models incorporate individual variability in K.) If the real level of individual variability in K was substantial, we might expect, on the basis of Sainsbury's (1980) observation, that models 3 and 4 would have given overestimates of μ_{L_∞} and underestimates of μ_K compared with models 6 and 7. Second, analyses of length-frequency modes suggest that the variance of length-at-age increases with increasing age (W.S. Hearn, CSIRO Div. Fish., GPO Box 1538, Hobart 7001, Aust., pers. commun.). This, as Sainsbury (1980) notes, is more the rule than the exception in fish populations, and is indicative of variation in L_∞ having the dominant effect on overall variation in length-at-age. Third, modes are clearly visible in the length-frequency data for at least the first four age-classes (Kirkwood 1983). Majkowski et al. (1987) give a general condition for the visual or statistical separability of length-frequency modes as $|\mu_i - \mu_{i-1}| < 2\min(\sigma_i, \sigma_{i+1})$, where μ_i and σ_i are the mean length and its standard deviation, respectively, of age-class i. Applying this condition to the mean-length and standard-deviation-at-age data given in Table 2, we find that only for models 3 and 4 (no variation in K) and models 6 and 7 ($\sigma_K/\mu_K = 0.07$) is the condition satisfied for separating age-classes 3 and 4. On this basis, we could conclude that the visibility of at least four modes in the length-frequency data would preclude levels of K variability much greater than those derived for models 6 and 7.

The problem of selecting the most appropriate model for use in stock assessment was addressed, using likelihood ratio tests. These indicated that model 1 was inadequate, and that a significantly better description of the data was provided by incorporating individual variation in L_∞ (model 3). However, the incorporation of individual variation in K or release-length-measurement error could not be justified.

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Estimation of Southern Bluefin Tuna *Thunnus maccoyii* Natural Mortality and Movement Rates from Tagging Experiments

John Hampton

CSIRO Division of Fisheries, Marine Laboratories
GPO Box 1538, Hobart, Tasmania 7001, Australia
Present address: South Pacific Commission, B.P. D5, Noumea Cedex, New Caledonia

Abstract.—Two models were fit to data from four experiments in which tagged southern bluefin tuna *Thunnus maccoyii* were released in Australian coastal waters and recaptured in the Australian surface fisheries and the Japanese longline fishery. The principal objective of the analysis was to estimate the instantaneous rate of natural mortality (M). Movement rates and catchability coefficients were also estimated using the second model. The first model (HSH) was fit to exact recapture times assuming, *inter alia*, that the tagged population was extinct at the time of the last tag return. The second model (SE) was fit to grouped data classified by two release fisheries and three recapture fisheries, explicitly incorporating movement between the geographically separated release fisheries and permanent emigration from the release fisheries into the Japanese longline fishery. Using the HSH model, estimates of M ranged from 0.20 to 0.42/year for the different experiments if full reporting of recaptured tags was assumed. The estimates decreased slightly as assumed reporting rate was decreased. The SE model yielded estimates of M ranging from 0.20 to 0.23/year with M constrained to be equal in each of the recapture fisheries. Unconstrained-M estimates were obtained which suggested higher levels of natural mortality in the release fisheries; however, these estimates were considered unreliable because of their large standard errors and high degree of confounding with other parameters of the model. Simulation trials indicated that input parameters used to generate simulated tag-return data sets could be accurately retrieved using the SE model. However, the HSH model produced positively biased estimates of M because of the low level of apparent fishing mortality in the Japanese longline fishery.

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The rate at which members of a fish population die from causes other than fishing, the so-called instantaneous rate of natural mortality (M), has a large bearing on the population and fishery dynamics of an exploited species. Natural death is rarely directly observable in fish populations, making M notoriously difficult to estimate, and much attention has been given over the years to devising experimental and statistical techniques to do so. The experimental technique most frequently used is tagging and recapture, the object of which, as stated by Beverton and Holt (1957), is "...to set up and examine the properties of an 'experimental' population of marked fish in which certain parameters that would be difficult or impossible to estimate in the 'natural' population can be determined with some accuracy".

A variety of statistical techniques has been developed to estimate M and other parameters from tagging experiments. One of the simplest is that of Gulland (1955), who derived maximum likelihood estimators for M and the fishing mortality rate (F) (both assumed constant over time) for a completed tagging experiment (i.e., one in which no tagged fish remain alive at the time of the last tag recapture). Hearn et al. (1987) generalized the Gulland (1955) method by allowing F to vary with time. Other models based on log-linear regression (Sandland 1982) or maximum likelihood estimation (Seber 1973, Wetherall 1982) normally require M and F to be constant; however, some of the more sophisticated methods allow F to vary with time as a function of fishing effort or catch (e.g., Lucas 1975, Kleiber et al. 1987). As an extension of these single-fishery models, Sibert (1984) developed a two-fishery model in which estimates of M, F, and the rates of movement between the fisheries could be obtained.

The southern bluefin tuna *Thunnus maccoyii* for many years has been the subject of an important fishery in southern Australian waters, where juveniles form surface schools and are captured principally by pole-and-line and purse-seine gears. In addition, a large fleet of Japanese longliners has targeted the adults in the higher, southern latitudes of the Indian, Southern, Pacific, and Atlantic Oceans since 1952.

Tagging experiments conducted by the Australian Commonwealth Scientific and Industrial Research Organization (CSIRO) have demonstrated that these fisheries exploit a common stock (Hampton 1989), and that there is considerable movement of juvenile fish between fishing grounds off the south coast of western Australia (WA), in the Great Australian Bight off south Australia (SA), and off the south coast of New South Wales (NSW). Throughout the juvenile phase, southern bluefin move away from the Australian coast and subsequently become recruited to the Japanese longline fishery (Fig. 1).

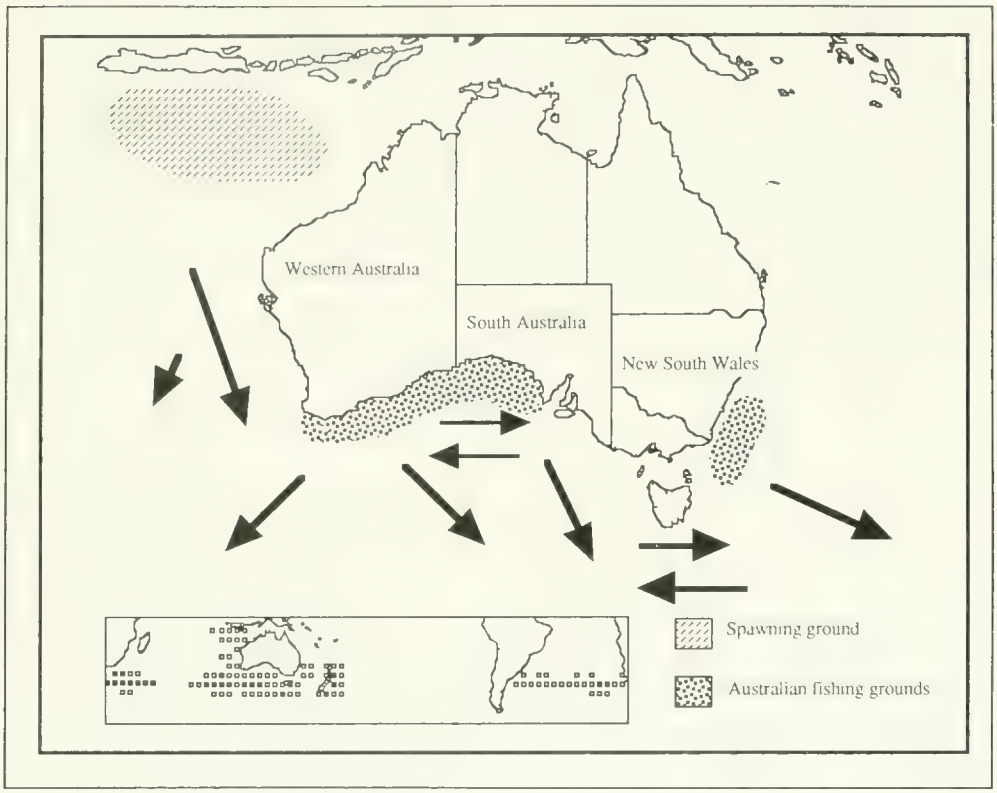


Figure 1
Geographical distribution of the Australian and Japanese (inset) southern bluefin tuna fisheries. Arrows indicate movement of fish in and away from Australian coastal waters. Black squares on the inset map indicate areas of higher Japanese catch.

During the 1980s, scientists became concerned that the fishery was being overexploited, and recent stock assessments have indicated the possibility that a decline in recruitment to the surface fishery could have occurred (Caton et al. 1990). These stock assessments have been based almost exclusively on cohort analysis (Gulland 1965) and other age-structured models, all of which require an estimate of M.

Despite its importance in stock assessment, the natural mortality rate of southern bluefin tuna has never been investigated in detail. Hayashi et al. (1969) considered a value of 0.2/year to be appropriate, based on a somewhat *ad hoc* comparison with growth parameter estimates. This value of M has been preferred in most stock assessments, although a range of values has also been used at various times (e.g., Hampton et al. 1984, Hampton and Majkowski 1986). More recently, the application of the Hearn et al. (1987) method to southern bluefin tagging data suggested that M could be somewhat higher than the "traditional" value of 0.2/year, possibly in excess of 0.4/year. However, the authors acknowledged that this was probably an overestimate because of likely non-compliance with various assumptions.

In this paper, selected southern bluefin tuna tagging experiments are analysed for the purpose of deriving estimates of M consistent with the tagging data. The Hearn et al. (1987) model (referred to as the HSH model) and an extension of the Sibert (1984) model (referred to as the SE model), which also provides estimates of movement rates between geographically separated fisheries and catchability coefficients, are applied. These models are tested using a simulation model that reflects characteristics of the southern bluefin population and fisheries.

Tagging data

Between 1959 and 1984, the CSIRO supervised the tagging of more than 60,000 southern bluefin tuna, mostly aged 2–4 years, of which approximately 12,000 have been recaptured and the tags returned. From these data, four tagging experiments from which no further returns are expected were defined (Table 1). Although other groupings of the tagging data are possible, the experiments were defined in this way so that they represent reasonably homogeneous groups in terms of release area, size of tagged fish, time period of release, fishing method, and tagging personnel involved. All fish were double-tagged using methods described by Williams (1982). All returns from these experiments were included in the analyses, with best estimates of recapture times (normally the midpoint of the fishing

Table 1

Southern bluefin tuna double-tagging experiments off Australia. NSW = off south coast of New South Wales; SA = Great Australian Bight off South Australia; WA = off south coast of Western Australia.

Experiment no.	Area	Years	Carried out by	Fishing method	No. released	No. recovered
1	NSW	1963–70	CSIRO	Pole-and-line	2770	433
2	NSW	1963–70	Fishermen under contract to CSIRO	Troll	9513	4205
3	SA	1964–69	CSIRO	Pole-and-line	7328	1276
4	WA	1963–67	CSIRO	Pole-and-line	12826	563

season) used for those returns where an exact recapture time was not available. The numbers of such returns were relatively few (experiment 1: 27, experiment 2: 114, experiment 3: 47, experiment 4: 35.

Methods of analysis

General assumptions of tagging experiments

Before describing the analytical methods used in this study, some discussion of general assumptions required for the estimation of mortality rates from tag-return data is warranted. These assumptions relate mostly to accounting for all forms of tag loss. In particular, tag losses due to tag shedding, tagging-induced mortality (e.g., through infection, or increasing the probability of predation or capture), and non-reporting of recovered tags must be absent or accounted for. This is frequently achieved by carrying out separate experiments to estimate parameters of models that describe these processes, e.g., double-tagging experiments to estimate tag-shedding rates, holding-tank experiments to test for tagging-induced mortality, and tag-seeding experiments to estimate the proportion of recovered tags that are returned to the tagging authority. The approach taken in this paper was to account for tag shedding using estimates derived by Hampton and Kirkwood (1990), assume tagging-induced mortality to be absent on the basis of various field observations, and repeat the parameter estimations over a range of plausible tag-reporting rates.

In addition to assumptions regarding tag loss, for analyses that include parameters or data relating to the recapture fishery, it is necessary to assume that the tagged and untagged populations are equally vulnerable to capture from the moment of release. Compliance with these and other assumptions for the present application are discussed in a later section.

The HSH model

In addition to the assumptions regarding tag loss, it is assumed here that all recapture times are accurately known, M is constant, the experiment is completed (i.e., no tagged fish remain alive at the time of the last tag recapture), and all tagged fish remain vulnerable to the fishery through a possibly variable but ultimately non-zero level of fishing mortality. Cessation of fishing would violate the assumption of completion, while permanent emigration of tagged fish away from the fishery would violate the assumption of complete vulnerability.

Let N_0 fish be released and n recaptures recorded at times $t_1 < t_2 < \ldots t_n$ after release. If the above assumptions are satisfied, the natural mortality rate estimator, $\hat{M}$, is obtained by solving the equation, derived by Hearn et al. (1987),

$$N_0 - \sum_{i=1}^{n} e^{Mt_i} = 0, \qquad (1)$$

using a numerical method such as the Newton-Raphson (Courant 1937).

Tag shedding is accounted for by introducing for each return a correction factor, w_i, which is the probability of a tagged fish retaining at least one tag at time t_i. For double-tagging experiments,

$$w_i = Q(t_i)\,[2 - Q(t_i)], \qquad (2)$$

where $Q(t_i)$ is the probability of a tag being retained at time t_i after release. Tag-shedding models have been fit to double-tagging data for each of the experiments (Hampton and Kirkwood 1990), the results of which are given in Table 2.

The tag-shedding correction is incorporated into Equation (1) as follows:

$$N_0 - \sum_{i=1}^{n} \frac{e^{Mt_i}}{w_i} = 0. \qquad (3)$$

Similarly, the non-reporting of recaptured tagged fish can be allowed for if the fraction, R, of recaptured tagged fish actually reported to the tagging authority is known or assumed. Equation (3) then becomes

Table 2
Tag-shedding models and parameter estimates (from Hampton and Kirkwood 1990) used in the estimation of natural mortality rate and related parameters of southern bluefin tuna.

Experiment	Tag-shedding model	Parameter estimates λ	b	ρ
1	$Q(t) = \rho e^{-\lambda t}$	0.29		0.93
1	$Q(t) = \left[\frac{b}{b+\lambda t}\right]^{b}$	1.00	0.26	
2	$Q(t) = \rho e^{-\lambda t^{b}}$	0.17		0.98
3	$Q(t) = \left[\frac{b}{b+\lambda t}\right]^{1}$	0.78	0.26	
4	$Q(t) = \left[\frac{b}{b+\lambda t}\right]^{1/b}$	1.04	0.36	

$$N_0 R - \sum_{i=1}^{n} \frac{e^{M t_i}}{w_i} = 0.$$

If there is a long-term mortality associated with bearing tags, this will be incorporated into $\hat{M}$ and be indistinguishable from it. An initial mortality due to tagging simply reduces the effective number of releases; if known, it can be included in the model in an identical fashion to R.

As discussed in Hearn et al. (1987), an estimate of the standard error of $\hat{M}$ is not available by conventional means because the estimate is conditional on the distribution of the data t_i. There is also no guarantee that the estimator is unbiased. A statistical tool that is commonly used in applied statistics both to reduce the bias of an estimator and to provide an approximate standard error is the jackknife (Cox and Hinkley 1974). This technique is not described in detail here; suffice to say that it is based on N_0 separate estimates of M that are obtained by removing, in turn, each tagged fish (whether recaptured or not) from the data. The mean of these estimates is the jackknife estimate of M, and their standard error is the jackknife estimate of the standard error of $\hat{M}$.

The SE model: An extension of the Sibert model

This model, unlike the HSH model, is fit to data grouped into time intervals, rather than individual, exact recapture times. In common with traditional single-release tag-attrition models (as described in detail, for example, in Seber 1973 and Wetherall 1982) that have been used extensively in the analysis of mark-recapture data, the SE model is based on classical population dynamics theory, as embodied in the Baranov catch equation (Baranov 1918).

The SE model extends the work of Sibert (1984), who developed a method of analyzing a tagging experiment in which tagged fish are released (not necessarily simultaneously) into two geographically separate fisheries that interact through the movement of fish. Sibert accomplished this basically by adding a spatial dimension and incorporating movement rates into the Baranov catch equation. Tag returns and catch or effort from the two fisheries, by time interval, form the observations to which the model is fit, yielding estimates of movement rates between the two fisheries, and estimates of M, catchability coefficient (when effort is used), and average population size (when catch is used) for each fishery. Recently, Hilborn (1990) developed a model similar to Sibert's in terms of estimation of movement rates; however, natural mortality rate is not specified in the population dynamics and therefore cannot be estimated using the Hilborn model.

To facilitate analyses of southern bluefin tagging experiments, Sibert's two-fishery model is extended in this paper to incorporate a third recapture fishery (the Japanese longline fishery). It is now assumed that there is movement of tagged fish from fisheries 1 and 2 (the release fisheries) into fishery 3. Movement between fisheries 1 and 2 can take place in both directions, but movement into fishery 3 is assumed to be permanent, i.e., there is no possibility of movement back to either fishery 1 or 2 once a fish has moved to fishery 3. This restriction of the model is adopted to avoid the necessity of estimating two additional movement parameters about which little information is available in the absence of releases into fishery 3 (large-scale tagging in the longline fishery is not feasible for southern bluefin tuna). However, this assumption is consistent with the known migratory behavior and the age composition of catches of southern bluefin from the Australian and Japanese fisheries (Hampton 1989).

In addition to the normal assumptions regarding tag loss, equal vulnerability of tagged and untagged fish must be assumed since catch and/or effort statistics are required for the analysis. It is also assumed, for simplicity, that M is constant over time within recapture fisheries.

Model derivation Following release, the tagged fish fall into six categories: the numbers released into fishery 1 that are at large in fishery 1 (N_{11}), fishery 2 (N_{12}), and fishery 3 (N_{13}), and the numbers released into fishery 2 that are at large in fishery 1 (N_{21}),

fishery 2 (N_{22}), and fishery 3 (N_{23}). The way in which these quantities change over time can be represented by six simultaneous differential equations (assuming, for the moment, that tag losses due to tag shedding, tag-induced mortality, and non-reporting are absent):

$$\frac{dN_{11}}{dt} = -(M_1 + F_1 + T_{12})N_{11} + T_{21}N_{12} \qquad (\text{at } t = 0,\ N_{11} = N_{01})$$

$$\frac{dN_{12}}{dt} = -(M_2 + F_2 + T_{21})N_{12} + T_{12}N_{11} \qquad (\text{at } t = 0,\ N_{12} = 0),$$

$$\frac{dN_{13}}{dt} = -(M_3 + F_3)N_{13} + T_{13}N_{11} + T_{23}N_{12} \qquad (\text{at } t = 0,\ N_{13} = 0),$$

$$\frac{dN_{21}}{dt} = -(M_1 + F_1 + T_{12})N_{21} + T_{21}N_{22} \qquad (\text{at } t = 0,\ N_{21} = 0),$$

$$\frac{dN_{22}}{dt} = -(M_2 + F_2 + T_{21})N_{22} + T_{12}N_{21} \qquad (\text{at } t = 0,\ N_{22} = N_{02}),$$

$$\frac{dN_{23}}{dt} = -(M_3 + F_3)N_{23} + T_{23}N_{22} + T_{13}N_{21} \qquad (\text{at } t = 0,\ N_{23} = 0), \qquad (4)$$

where N_{01} and N_{02} are the number of releases into the two fisheries, M_1, M_2, and M_3 are the rates of natural mortality operating in the three fisheries, F_1, F_2, and F_3 are the rates of fishing mortality specific to the three fisheries (assumed, for the moment, to be constant over time), and T_{12}, T_{13}, T_{21}, and T_{23} are movement rates (the first subscript denoting the donor fishery and the second subscript denoting the recipient fishery).

Tag returns from the three fisheries can be classified in a similar fashion to numbers at large, i.e., r_{11}, r_{12}, and r_{13} are the numbers of returns of fish released in fishery 1 that are recaptured in fisheries 1, 2, and 3, respectively, and r_{21}, r_{22}, and r_{23} are the numbers of returns of fish released in fishery 2 that are recaptured in fisheries 1, 2, and 3, respectively. The estimated rates of return in these categories can be written as:

$$\frac{d\hat{r}_{11}}{dt} = F_1N_{11},$$

$$\frac{d\hat{r}_{12}}{dt} = F_2N_{12},$$

$$\frac{d\hat{r}_{13}}{dt} = F_3N_{13},$$

$$\frac{d\hat{r}_{21}}{dt} = F_1N_{21},$$

$$\frac{d\hat{r}_{22}}{dt} = F_2N_{22},$$

and

$$\frac{d\hat{r}_{23}}{dt} = F_3N_{23}. \qquad (5)$$

Equations (4) and (5) are solved by integrating between times t and $t+\Delta t$. For ease of notation, define $A_1 = M_1 + F_1 + T_{12} + T_{13}$, $A_2 = M_2 + F_2 + T_{21} + T_{23}$, and $A_3 = M_3 + F_3$. Integrating Equations (4) is accomplished by applying a decoupling transformation (see Sibert 1984 for details) and results in the following set of delay-difference equations,

$$N_{11(t+\Delta t)} = \frac{1}{1+ab}\{a[bN_{11(t)} + N_{12(t)}]\, e^{-u\Delta t} + [N_{11(t)} - aN_{12(t)}]\, e^{-v\Delta t}\},$$

$$N_{12(t+\Delta t)} = \frac{1}{1+ab}\{[bN_{11(t)} + N_{12(t)}]\, e^{-u\Delta t} - b[N_{11(t)} - aN_{12(t)}]\, e^{-v\Delta t}\},$$

$$N_{13(t+\Delta t)} = N_{13(t)}\, e^{-A_3\Delta t} + \frac{T_{13}}{A_1-A_3} N_{11(t)}[e^{-A_3\Delta t} - e^{-A_1\Delta t}] + \frac{T_{23}}{A_2-A_3} N_{12(t)}[e^{-A_3\Delta t} - e^{-A_2\Delta t}],$$

$$N_{21(t+\Delta t)} = \frac{1}{1+ab}\{a[N_{22(t)} + bN_{21(t)}]\, e^{-u\Delta t} + [N_{22(t)} - aN_{22(t)}]\, e^{-v\Delta t}\},$$

$$N_{22(t+\Delta t)} = \frac{1}{1+ab}\{[N_{22(t)} + bN_{21(t)}]\, e^{-u\Delta t} - b[N_{21(t)} - aN_{22(t)}]\, e^{-v\Delta t}\},$$

and

$$N_{23(t+\Delta t)} = N_{23(t)}\, e^{-A_3\Delta t} + \frac{T_{23}}{A_2-A_3} N_{22(t)}[e^{-A_3\Delta t} - e^{-A_2\Delta t}] + \frac{T_{13}}{A_1-A_3} N_{21(t)}[e^{-A_3\Delta t} - e^{-A_1\Delta t}], \qquad (6)$$

where a and b, the coefficients of the decoupling transformation, are roots of two quadratic equations,

$$T_{12}a^2 - (A_2-A_1)a - T_{21} = 0, \qquad T_{21}b^2 - (A_2-A_1)b - T_{12} = 0,$$

and

$$v = \frac{A_1+bT_{21}+abA_2+aT_{12}}{1+ab}, \qquad u = \frac{A_2-aT_{12}+abA_1-bT_{21}}{1+ab}.$$

Substituting Equations (6) into Equations (5) and integrating, the estimated numbers of tagged fish of each category recaptured between times t and $t+\Delta t$ are obtained:

$$\hat{r}_{11(t)} = \frac{R_1F_1}{1+ab}\left\{a\left[\frac{bN_{11(t)}+N_{12(t)}}{u}\right](1-e^{-u\Delta t}) + \left[\frac{N_{11(t)}-aN_{12(t)}}{v}\right](1-e^{-v\Delta t})\right\},$$

$$\hat{r}_{12(t)} = \frac{R_2F_2}{1+ab}\left\{\left[\frac{bN_{11(t)}+N_{12(t)}}{u}\right](1-e^{-u\Delta t}) - b\left[\frac{N_{11(t)}-aN_{12(t)}}{v}\right](1-e^{-v\Delta t})\right\},$$

$$\hat{r}_{13(t)} = R_3F_3\left\{\left[\frac{T_{13}}{A_1-A_3}N_{11(t)}+N_{13(t)}\right]\frac{(1-e^{-A_3\Delta t})}{A_3} - \frac{T_{13}}{A_1-A_3}N_{11(t)}\frac{(1-e^{-A_1\Delta t})}{A_1}\right\},$$

$$\hat{r}_{21(t)} = \frac{R_1F_1}{1+ab}\left\{a\left[\frac{N_{22(t)}+bN_{21(t)}}{u}\right](1-e^{-u\Delta t}) + \left[\frac{N_{21(t)}-aN_{22(t)}}{v}\right](1-e^{-v\Delta t})\right\},$$

$$\hat{r}_{22(t)} = \frac{R_2 F_2}{1+ab}\left\{\left[\frac{N_{22(t)}+bN_{21(t)}}{u}\right](1-e^{-u\Delta t}) - b\left[\frac{N_{21(t)}-aN_{22(t)}}{v}\right](1-e^{-v\Delta t})\right\},$$

and

$$\hat{r}_{23(t)} = R_3 F_3\left\{\left[\frac{T_{23}}{A_2-A_3}N_{22(t)}+N_{23(t)}\right]\frac{(1-e^{-A_3\Delta t})}{A_3} - \frac{T_{23}}{A_2-A_3}N_{22(t)}\frac{(1-e^{-A_2\Delta t})}{A_2}\right\}. \quad (7)$$

Equations (6) and (7) describe the dynamics of tagged fish as a function of the parameters M_1, M_2, M_3, F_1, F_2, F_3, T_{12}, T_{13}, T_{21}, and T_{23}. Fishery-specific reporting rates, R_1, R_2, and R_3, have been introduced and are assumed known. The tag-shedding correction factor, w_t, (Eq. 2) can be introduced in a similar fashion to R (i.e., as a multiplier of F). Note that w_t now refers to the probability of retaining at least one tag at the midpoint of period $t + \Delta t$ and may differ according to fishery of release.

In practice, it is likely that the Fs will vary with time. If catch or effort data are available by time period (indexed by i), F_1, F_2, and F_3 can be reparameterized as

$$F_{1i} = q_1 f_{1i} \sim \frac{C_{1i}}{P_1},$$

$$F_{2i} = q_2 f_{2i} \sim \frac{C_{2i}}{P_2},$$

$$F_{3i} = q_3 f_{3i} \sim \frac{C_{3i}}{P_3}, \quad (8)$$

where q_1, q_2, and q_3 are catchability coefficients for the three fisheries, f_{1i}, f_{2i}, and f_{3i} are the fishing efforts in the three fisheries in time period i, P_1, P_2, and P_3 are mean population sizes available to the three fisheries over the course of the tagging experiment, and C_{1i}, C_{2i}, and C_{3i} are catches in the three fisheries during period i (expressed in the same units as P). Variable F can now be accommodated without the addition of extra parameters to the model. This, as noted above, involves the assumption that the tagged and untagged fish are equally vulnerable from the moment of release. The choice of which parameterization to use will ultimately depend on the data available and how one views the relationship between catch, effort, catchability, and population size. In fisheries for surface schooling tunas, effective effort is extremely difficult to quantify, and no such estimates are available for the southern bluefin fisheries. For this reason, I have preferred the parameterization using catch in this paper, although for ease of presentation of simulation results, this has been done by assuming the catch to be an index of effective effort and estimates of q, rather than P, obtained. (By so doing, P is in fact the reciprocal of q.) Note that Equations (8) are approximations in the case of catch data, and require that the populations be close to equilibrium for unbiased estimates to be obtained.

Sibert (1984) used a least-squares technique to obtain estimates of the various parameters for the two-fishery model, and employed a square-root transformation as a weighting scheme for observations within the four tag-recovery categories. Several methods of weighting the four individual sums of squares were also tested. Difficulties can arise in choosing the most appropriate weighting scheme, both for observations within and between return categories. These problems can be avoided by using a maximum-likelihood technique based on multinomial probabilities (Seber 1973). Here, a likelihood function can be constructed for each fishery of tag release, e.g., for releases into fishery 1,

$$f_1(\{r_{11(i)}, r_{12(i)}, r_{13(i)}\}) = \frac{N_{01}!\,(1-Pr_1)^{N_{01}-n_1}\prod_{i=1}^{k}\{p_{11(i)}^{r_{11(i)}}\,p_{12(i)}^{r_{12(i)}}\,p_{13(i)}^{r_{13(i)}}\}}{\left\{\prod_{i=1}^{k} r_{11(i)}!\,r_{12(i)}!\,r_{13(i)}!\right\}(N_{01}-n_1)!},$$

where n_1 is the total number of returns from fishery 1 releases, up to and including period k, $p_{11(i)}$ is the probability of recovery in fishery 1 during period i ($p_{11(i)} = \frac{\hat{r}_{11(i)}}{N_{01}}$), $p_{12(i)}$ is the probability of recovery in fishery 2 during

period i ($p_{12(i)} = \frac{\hat{r}_{12(i)}}{N_{01}}$), $p_{13(i)}$ is the probability of recovery in fishery 3 during period i ($p_{13(i)} = \frac{\hat{r}_{13(i)}}{N_{01}}$), and

$$Pr_1 = \sum_{i=1}^{k} p_{11(i)} + p_{12(i)} + p_{13(i)}.$$

An equivalent function, $f_2(\{r_{21(i)}, r_{22(i)}, r_{23(i)}\})$ can be written for releases into fishery 2. Estimates of parameters may then be found by minimizing

$$L = -\log_e [f_1(\{r_{11(i)}, r_{12(i)}, r_{13(i)}\}) \cdot f_2(\{r_{21(i)}, r_{22(i)}, r_{23(i)}\})]$$

with an estimate of the variance-covariance matrix found using the inverse-Hessian method (Bard 1974).

Simulation trials using the model described below showed that unbiased results are obtained using the maximum-likelihood technique, whereas unbiased results could not be guaranteed with the least-squares approach. In the applications of the SE method presented here, the maximum-likelihood estimation technique is used.

Simulation model

In order to examine the behavior of the HSH and SE estimates, a simulation model was developed. The simulation model determines the fate of each tagged fish released into the two fisheries in a probabilistic fashion. For the moment, consider only releases into fishery 1. During the first time period after release, a tagged fish will either:

(i) be recaptured in fishery 1;
(ii) die from natural causes in fishery 1;
(iii) survive in fishery 1 to the end of the first period and then be subject to all possibilities in the next time period;
(iv) migrate to fishery 2 at time $x<1$;
(v) migrate to fishery 3 at time $x<1$;
(vi) given (iv), be recaptured in fishery 2 at time y ($x<y<1$);
(vii) given (iv), die from natural causes in fishery 2 at time y ($x<y<1$);
(viii) given (iv), survive in fishery 2 until the end of time period 1 and then be subject to possibilities (vi) through (x) in the next time period;
(ix) given (iv), migrate back to fishery 1 at time y ($x<y<1$) and then be subject to all possibilities for the remainder of time period 1;
(x) given (iv), migrate to fishery 3 at time y ($x<y<1$) and then be subject to possibilities (xi) through (xiii) in fishery 3 for the remainder of time period 1;
(xi) given (v), be recaptured in fishery 3 at time y ($x<y<1$);
(xii) given (v), die from natural causes in fishery 3 at time y ($x<y<1$);
(xiii) given (v), survive in fishery 3 until the end of time period 1 and then be subject to possibilities (xi) through (xiii) in the next time period.

The probabilities of each of these events occurring are (omitting, for convenience, the time subscript):

$$P(i) = [1-e^{-A_1}]\frac{F_1}{A_1},$$

$$P(ii) = [1-e^{-A_1}]\frac{M_1}{A_1},$$

$$P(iii) = e^{-A_1},$$

$$P(iv) = [1-e^{-A_1}]\frac{T_{12}}{A_1},$$

$$P(v) = [1-e^{-A_1}]\frac{T_{13}}{A_1},$$

$$P(vi) = P(iv) \cdot [1-e^{-A_2(1-x)}]\frac{F_2}{A_2},$$

$$P(vii) = P(iv) \cdot [1-e^{-A_2(1-x)}]\frac{M_2}{A_2},$$

$$P(viii) = P(iv) \cdot e^{-A_2(1-x)},$$

$$P(ix) = P(iv) \cdot [1-e^{-A_2(1-x)}]\frac{T_{21}}{A_2},$$

$$P(x) = P(iv) \cdot [1 - e^{-A_2(1-x)}] \frac{T_{23}}{A_2},$$

$$P(xi) = P(v) \cdot [1 - e^{-A_3(1-x)}] \frac{F_3}{A_3},$$

$$P(xii) = P(v) \cdot [1 - e^{-A_3(1-x)}] \frac{M_3}{A_3},$$

and

$$P(xiii) = P(v) \cdot e^{-A_3(1-x)}.$$

F_1, F_2, and F_3 may be allowed to vary by specifying a constant q or P and dependent f or C (as per Equations 8). An identical process deals with releases into fishery 2.

To determine which of the possible outcomes (i) to (v) first befalls a tagged fish, a pseudorandom number, α, uniformly distributed on [0,1] is generated using a computer subroutine (e.g., subroutine URAND given in Forsythe et al. 1977:245). If $\alpha < P(i)$, outcome (i) is chosen; if $P(i) < \alpha < [P(i) + P(ii)]$, outcome (ii) is chosen; if $[P(i) + P(ii)] < \alpha < [P(i) + P(ii) + P(iii)]$, outcome (iii) is chosen; and so on. Additional pseudorandom numbers are generated and further tests relating to outcomes (vi) to (xiii) applied as necessary until the fish is deemed to have been recaptured, died naturally, or survived to the end of the experiment. When the fates of all tagged fish released into both fisheries are determined in this way, the six tag-return vectors, r_{11}, r_{12}, r_{13}, r_{21}, r_{22}, and r_{23} are established. The SE model can then be fit to these data and the estimated parameter values compared with the "real" values input to the simulation model. The HSH model can be similarly tested, with exact recapture times within the determined period of capture simulated by randomly sampling from a truncated exponential distribution (truncated at one year in this case) as shown in Hearn et al. (1987).

Results

HSH model

The jackknife estimates of M and their standard errors obtained by fitting the HSH model to data from experiments 1–4 are given in Table 3. If full reporting of tags is assumed, the estimates of M range from just less than 0.2/year to just more than 0.4/year; the estimates decrease slightly as reporting rate decreases.

It is clear that the tag-shedding model used to weight the returns has a large bearing on the estimate of M obtained. For experiment 2, the best fitting tag-shedding model (constant shedding rate) predicts a very low probability of tag retention after long periods at liberty (Hampton and Kirkwood 1990). Therefore, those returns from the Japanese fishery at liberty for longer than, say, 6 years will receive large weight in the analysis using the HSH method; this is one of the main reasons for the relatively low estimate of M (0.2275/year for a reporting rate of 1.0). In contrast, a decreasing tag-shedding rate model provided the best fit to the double-tagging data from experiments 3 and 4. Here, there is little change in the probability of tag retention after about 3 or 4 years at liberty (Hampton and Kirkwood 1990). All returns after this time will, then, receive similar weight from the tag-shedding model; accordingly, relatively high estimates of M are obtained for experiments 3 and 4 (0.4165/year and 0.4163/year, respectively, for a reporting rate of 1.0). The most direct test of the effect of the different tag-shedding models is the application of both constant and decreasing shedding-rate models to the analysis of experiment 1 (these tag-shedding models provided equally good fits to experiment 1 double-tagging data, and could not be distinguished on the statistical criterion used by Hampton and Kirkwood 1990). Here, the estimate of M obtained when the constant shedding-rate model was used

Table 3

Estimates of the rate of natural mortality (M) and their standard errors (SE) for different reporting rates (R) obtained from fitting the HSH model to data from experiments 1–4 (see Table 1 for descriptions). Separate estimates are given for two tag-shedding models derived for experiment 1. All estimates are in units per year.

	Experiment 1				Experiment 2		Experiment 3		Experiment 4	
	Constant shedding rate		Decreasing shedding rate		Constant shedding rate		Decreasing shedding rate		Decreasing shedding rate	
R	M	SE	M	SE	M	SE	M	SE	M	SE
1.0	0.1987	0.0681	0.4038	0.0634	0.2275	0.1740	0.4165	0.0860	0.4163	0.0646
0.9	0.1896	0.0674	0.3941	0.0625	0.2239	0.1604	0.4091	0.0815	0.4098	0.0633
0.8	0.1792	0.0665	0.3827	0.0613	0.2194	0.1420	0.4002	0.0763	0.4023	0.0619
0.7	0.1669	0.0654	0.3693	0.0599	0.2122	0.1158	0.3891	0.0702	0.3937	0.0601
0.6	0.1519	0.0640	0.3527	0.0580	0.1965	0.0733	0.3748	0.0628	0.3835	0.0581
0.5	0.1330	0.0620	0.3312	0.0553	0.1148	0.0205	0.3549	0.0538	0.3710	0.0556

(0.1987/year for a reporting rate of 1.0) is less than half the estimate obtained when the decreasing shedding-rate model was used (0.4038/year for a reporting rate of 1.0).

SE model

The SE model was fit to the tag-return data from experiments 2 and 3 (analysis A) and experiments 2 and 4 (analysis B). These data, along with the catch data used to parameterize Fs, are shown in Tables 4 and 5, respectively. For analysis A, returns from the NSW fishery (fishery 1) were defined by recapture positions east of 145°E. SA fishery (fishery 2) returns were defined by recapture positions west of 145°E. No returns from these experiments were recorded in WA (defined for these purposes as west of 125°E) as commercial tuna fishing in WA did not begin until 1969. For analysis B, there is a slight complicating factor in that southern bluefin were tagged in WA before substantial commercial fishing began in 1969; the majority of the few returns recorded in WA from experiment 4 were from the tagging vessel. However, because the tagged fish were released in the WA area, fishery 2 for analysis B is defined as the SA and WA areas combined. For both analyses, fishery 3 is the Japanese longline fishery with no geographical restrictions.

As mentioned earlier, the use of catch data to parameterize F involves an assumption that the population is in equilibrium for the duration of the tag-recovery period. This is not an unreasonable assumption for the juvenile population available to the surface

Table 4

Numbers of tag returns from experiment 2 and experiment 3 by period at liberty and related catch statistics used in analysis A of the SE model. NSW (fishery 1) and SA (fishery 2) catches are 8-year moving averages beginning 1963–70 for NSW and 1964–71 for SA. The Japanese (fishery 3) catch used is the 1964–85 average. NSW = off south coast of New South Wales; SA = Great Australian Bight off South Australia.

Time at liberty (yr)	Experiment 2 releases (NSW) Returns from			Experiment 3 releases (SA) Returns from			Catches ($t \times 10^3$)		
	NSW	SA	Japan	NSW	SA	Japan	NSW	SA	Japan
0–1	3144	55	4	159	842	14	3.445	3.968	45.216
1–2	854	24	12	37	77	24	3.748	3.825	45.216
2–3	64	8	17	7	3	28	4.232	4.089	45.216
3–4	5	0	4	0	0	23	4.177	4.213	45.216
4–5	0	0	2	0	0	23	4.569	4.395	45.216
5–6	2	0	0	0	0	12	4.418	4.896	45.216
6–7	0	0	3	0	0	9	3.815	5.588	45.216
7–8	0	0	2	0	0	3	3.681	5.815	45.216
8–9	0	0	1	0	0	8	3.772	6.005	45.216
9–10	0	0	1	0	0	3	3.594	6.315	45.216
10–11	0	0	2	0	0	1	3.256	6.695	45.216
11–12	0	0	0	0	0	2	3.438	7.415	45.216
12–13	0	0	0	0	0	0	2.984	8.539	45.216
13–14	0	0	0	0	0	0	2.788	8.974	45.216
14–15	0	0	0	0	0	0	2.764	9.284	45.216
15–16	0	0	0	0	0	0	2.163	10.178	45.216
16–17	0	0	1	0	0	1	1.626	10.856	45.216

Table 5

Numbers of tag returns from experiment 2 and experiment 4 by period at liberty and related catch statistics used in analysis B of the SE model. NSW (fishery 1) and SA (fishery 2) catches are 8-year moving averages beginning 1963–70 for NSW and 1964–71 for SA. The Japanese (fishery 3) catch used is the 1964–85 average. NSW = off south coast of New South Wales; SA = Great Australian Bight off South Australia; WA = off south coast of Western Australia.

Time at liberty (yr)	Experiment 2 releases (NSW) Returns from			Experiment 4 releases (WA) Returns from			Catches ($t \times 10^3$)		
	NSW	SA/WA	Japan	NSW	SA/WA	Japan	NSW	SA/WA	Japan
0–1	3144	55	4	37	220	6	3.445	4.094	45.216
1–2	854	24	12	109	75	3	3.748	4.026	45.216
2–3	64	8	17	12	11	28	4.232	4.385	45.216
3–4	5	0	4	0	1	10	4.177	4.547	45.216
4–5	0	0	2	0	0	21	4.569	4.763	45.216
5–6	2	0	0	1	0	14	4.418	5.407	45.216
6–7	0	0	3	0	0	5	3.815	6.148	45.216
7–8	0	0	2	0	0	0	3.681	6.443	45.216
8–9	0	0	1	0	0	4	3.772	6.775	45.216
9–10	0	0	1	0	0	1	3.594	7.299	45.216
10–11	0	0	2	0	0	0	3.256	7.879	45.216
11–12	0	0	0	0	0	1	3.438	8.914	45.216
12–13	0	0	0	0	0	0	2.984	10.481	45.216
13–14	0	0	0	0	0	2	2.788	11.768	45.216
14–15	0	0	0	0	0	0	2.764	12.283	45.216
15–16	0	0	0	0	0	1	2.163	13.334	45.216
16–17	0	0	1	0	0	0	1.626	13.925	45.216
17–18	0	0	0	0	0	1	1.175	13.353	45.216

Table 6

Estimates of parameters and their standard errors (SE) for different reporting rates, resulting from fitting the SE model (analysis A: unconstrained Ms) to data from experiments 2 and 3 (Table 4). All mortality and movement parameters are in units per year.

	Reporting rate					
	1.0		0.9		0.8	
Parameter	Estimate	SE	Estimate	SE	Estimate	SE
M_1	0.7135	0.4354	0.6336	0.5673 E-1	0.5295	0.1105
M_2	0.1490 E+1	0.2555 E+1	0.1449 E+1	0.3114	0.1391 E+1	0.6542
M_3	0.2044	0.1264	0.2019	0.2636 E-1	0.1975	0.4307 E-1
q_1	0.2046	0.4249 E-2	0.2267	0.4705 E-2	0.2544	0.5276 E-2
q_2	0.8595 E-1	0.4330 E-2	0.9512 E-1	0.4806 E-2	0.1072	0.5397 E-2
q_3	0.6147 E-3	0.2762 E-2	0.6912 E-3	0.4003 E-3	0.7526 E-3	0.8415 E-3
T_{12}	0.1176	0.1330 E-1	0.1182	0.1347 E-1	0.1169	0.1322 E-1
T_{13}	0.9667 E-1	0.4348	0.9452 E-1	0.5432 E-1	0.9758 E-1	0.1092
T_{21}	0.1750	0.1435 E-1	0.1751	0.1437 E-1	0.1750	0.1437 E-1
T_{23}	0.5691	0.2553 E+1	0.5637	0.3283	0.5784	0.6462
	0.7		0.6		0.5	
	Estimate	SE	Estimate	SE	Estimate	SE
M_1	0.3582	0.9196 E-1	0.2232	0.1346	0.8865 E-2	0.9048 E-1
M_2	0.1090 E+1	0.5488	0.1213 E+1	0.7968	0.1239 E+1	0.5315
M_3	0.2057	0.2837 E-1	0.1890	0.6001 E-1	0.1660	0.7660 E-1
q_1	0.2900	0.6015 E-2	0.3367	0.6969 E-2	0.4014	0.8306 E-2
q_2	0.1224	0.6177 E-2	0.1431	0.7218 E-2	0.1715	0.8655 E-2
q_3	0.6118 E-3	0.3980 E-3	0.9476 E-3	0.1225 E-2	0.1476 E-2	0.1649 E-2
T_{12}	0.1172	0.1326 E-1	0.1155	0.1312 E-1	0.1151	0.1301 E-1
T_{13}	0.1382	0.9035 E-1	0.1026	0.1339	0.7884 E-1	0.8817 E-1
T_{21}	0.1754	0.1440 E-1	0.1760	0.1441 E-1	0.1764	0.1443 E-1
T_{23}	0.8203	0.5449	0.6121	0.7933	0.4735	0.5314

fisheries as long as recruitment was reasonably constant during this period. The stability of the surface catches during the 1960s and early 1970s and cohort analysis (Hampton 1989) would suggest that this was the case. Although the adult population declined during several periods since exploitation began, Japanese catch was fairly constant during these tagging experiments, and parental biomass also appeared to be relatively stable. Therefore, the use of catch data to parameterize F should not cause major difficulties in this case.

In these experiments, tagged southern bluefin were released over a period of years; therefore, returns within a specific time-at-liberty category cannot be related to a catch in any one year. In these cases, the catch (or effort) data used are normally averaged over time, assuming a constant F within each fishery (e.g., Kleiber et al. 1987). This was the approach taken for the Japanese fishery, where catch was in fact quite constant over most of the return period (mid-1960s to early 1980s). For the Australian surface fisheries, an 8-year moving average (equivalent to the total release period for experiments 2, 3, and 4) was used so that the gradual decline of the NSW fishery and gradual increase in the SA and WA fisheries (Hampton 1989) could be represented.

Analysis A The first fit to the data allowed M to vary among the three fisheries. The resulting estimates of the three natural mortality parameters, three catchability parameters and four movement parameters and their standard errors, for reporting rates between 1.0 and 0.5, are presented in Table 6. There is no *a priori* reason why reporting rate should be the same for the three fisheries. In the absence of any information on the actual reporting rates, they have been assumed here, for simplicity, to be the same for the three fisheries.

For a reporting rate of 1.0, the estimates of M for the three fisheries are 0.71/year, 1.5/year, and 0.20/year, respectively. M_2 and M_3 decrease slightly as reporting rate decreases; however, M_1 decreases substantially with decreasing reporting rate. This is because the tag recapture rate in NSW is very high even if a reporting rate of 1.0 is assumed; therefore, even relatively small reductions in reporting rate from 1.0 require substantial compensatory changes in M_1.

Catchability in the NSW fishery is very high and suggests a fishing mortality rate of approximately 0.8/year, reflecting the high recapture rate there (33% of experiment 2 releases recaptured within 1 year and 42% recaptured within 2 years). Catchability is substantially lower in the SA and Japanese fisheries, suggesting rates of fishing mortality of approximately 0.35/year and 0.03/year, respectively. The catchability coefficients increase steadily with decreasing reporting rates, approximately doubling with a reduction in assumed reporting rate from 1.0 to 0.5. Rates of movement are slightly higher in the SA→NSW direction (0.17/year) than in the NSW→SA direction (0.12/year). Apparent movement into the Japanese fishery is substantially higher from the SA fishery (0.57/year) than from the NSW fishery (0.10/ year). The movement parameters are relatively unaffected by changing the assumed reporting rate within the range 1.0–0.5.

Table 7

Correlation matrix for parameter estimates resulting from fitting the SE model (analysis A: unconstrained Ms) to data from experiments 2 and 3 (Table 6) for a reporting rate of 1.0. The matrix was estimated by the inverse-Hessian method (Bard 1974).

Parameter	M_1	M_2	M_3	q_1	q_2	q_3	T_{12}	T_{21}	T_{13}	T_{23}
M_1	1.00									
M_2	0.99	1.00								
M_3	−0.98	−0.99	1.00							
q_1	0.01	−0.01	−0.01	1.00						
q_2	0.03	0.04	−0.03	−0.04	1.00					
q_3	0.99	0.99	−0.98	−0.01	0.02	1.00				
T_{12}	−0.06	−0.04	0.04	−0.09	−0.15	−0.04	1.00			
T_{21}	0.00	0.01	−0.01	−0.10	0.37	0.00	0.04	1.00		
T_{13}	−0.99	−0.99	0.98	0.01	−0.02	−0.99	−0.04	−0.00	1.00	
T_{23}	−0.99	−0.99	0.98	0.01	−0.02	−0.99	−0.04	0.00	0.99	1.00

The standard errors of the parameters are large, particularly for M_1, M_2, T_{13}, and T_{23}. The correlation matrix for the parameters (Table 7) indicates several cases of extreme confounding of estimates. The Ms are very highly correlated with one another and individually with q_3, T_{13}, and T_{23}. The latter three parameters are also very highly correlated with one another. These high correlations and standard errors suggest that the model is overdetermined (too many parameters).

Table 8

Estimates of parameters and their standard errors (SE) for different reporting rates, resulting from fitting the SE model (analysis A: constrained Ms) to data from experiments 2 and 3 (Table 4). All mortality and movement parameters are in units per year.

	Reporting rate					
	1.0		0.9		0.8	
Parameter	Estimate	SE	Estimate	SE	Estimate	SE
M	0.2299	0.2326 E−1	0.2288	0.2285 E−1	0.2278	0.2224 E−1
q_1	0.2042	0.4244 E−2	0.2263	0.4697 E−2	0.2543	0.5278 E−2
q_2	0.8616 E−1	0.4341 E−1	0.9560 E−1	0.4820 E−2	0.1075	0.5416 E−2
q_3	0.1614 E−3	0.1981 E−4	0.1912 E−3	0.2349 E−4	0.2363 E−3	0.2917 E−4
T_{12}	0.1230	0.1393 E−1	0.1215	0.1372 E−1	0.1204	0.1355 E−1
T_{21}	0.5705	0.3142 E−1	0.4906	0.3050 E−1	0.3922	0.2923 E−1
T_{13}	0.1749	0.1433 E−1	0.1748	0.1434 E−1	0.1748	0.1432 E−1
T_{23}	0.1848 E+1	0.9067 E−1	0.1805 E+1	0.8919 E−1	0.1756 E+1	0.8755 E−1
	0.7		0.6		0.5	
	Estimate	SE	Estimate	SE	Estimate	SE
M	0.2184	0.2061 E−1	0.1871	0.1717 E−1	0.1188	0.1360 E−1
q_1	0.2898	0.6007 E−2	0.3345	0.6881 E−2	0.3842	0.7657 E−2
q_2	0.1226	0.6181 E−2	0.1440	0.7239 E−2	0.1757	0.8793 E−2
q_3	0.2961 E−3	0.3617 E−4	0.3572 E−3	0.4162 E−4	0.3685 E−3	0.4209 E−4
T_{12}	0.1163	0.1295 E−1	0.1065	0.1164 E−1	0.8711 E−1	0.1536 E−1
T_{21}	0.2795	0.2638 E−1	0.1662	0.2031 E−1	0.8650 E−1	0.1259 E−1
T_{13}	0.1758	0.1440 E−1	0.1787	0.1458 E−1	0.1895	0.1536 E−1
T_{23}	0.1691 E+1	0.8503 E−1	0.1625 E+1	0.8109 E−1	0.1548 E+1	0.7539 E−1

Table 9

Correlation matrix for parameter estimates resulting from fitting the SE model (analysis A: constrained Ms) to data from experiments 2 and 3 (Table 8) for a reporting rate of 1.0. The matrix was estimated by the inverse-Hessian method (Bard 1974).

Parameter	M	q_1	q_2	q_3	T_{12}	T_{21}	T_{13}	T_{23}
M	1.00							
q_1	−0.02	1.00						
q_2	−0.04	−0.04	1.00					
q_3	0.81	−0.03	−0.06	1.00				
T_{12}	0.01	0.09	−0.16	0.05	1.00			
T_{21}	−0.02	−0.10	0.37	−0.02	−0.04	1.00		
T_{13}	−0.76	0.24	0.07	−0.65	−0.31	−0.05	1.00	
T_{23}	−0.30	−0.03	0.68	−0.26	0.06	0.39	0.17	1.00

Consequently, in the second fit to the data, M was assumed to be equal for the three fisheries (constrained M), thus reducing the number of parameters from ten to eight. A likelihood ratio test (Kendall and Stuart 1979) was conducted with the constrained-M fit defined as the null hypothesis and the unconstrained-M fit as the alternative hypothesis (assuming $R = 1.0$). The test indicated that the unconstrained-M fit was significantly better than the constrained-M fit ($P < 0.01$). However, the constrained-M fit resulted in much smaller standard errors for the critical parameters (Table 8); q_3 has a coefficient of variation (CV) of 15%, with all other parameters having CVs of less than 10%. The correlation among the parameters is also much more acceptable (Table 9), although M is still correlated to a degree with q_3 and T_{13}, as are the qs with their respective incoming and outgoing movement parameters.

There are substantial changes in some of the parameter estimates obtained from the constrained-M fit. The overall estimate of M is 0.23/year, which is similar to the estimate of M_3 obtained from the unconstrained-M fit, but is much smaller than the M_1 and M_2 estimates. There is little change in q_1, q_2, T_{12}, or T_{21}; however, T_{13} and T_{23} are much larger in the constrained-M fit. These higher values compensate for the reduced M_1 and M_2 estimates (now assumed equal to M_3) in order to maintain the observed high rate of attrition of tagged fish in the NSW and SA fisheries. With the higher movement rates into the Japanese fishery, q_3 is smaller in the constrained-M fit so that the observed rate of return of tags from that fishery is still well described by the model. The estimate of M is insensitive to reductions in reporting rate to about 0.7, while the other parameter estimates behave similarly to those of the unconstrained-M fit.

Plots of observed numbers of returns and the numbers expected on the basis of the constrained-M fit for each of the release-recapture categories do not reveal any glaring deficiencies in the model (Fig. 2). Plotting expected numbers of returns using the unconstrained-M fit produced an essentially identical result.

Analysis B The results of the unconstrained-M fits to the results of experiments 2 and 4 are given in Table 10. The estimate of M_1 is substantially smaller (0.28/year) than that obtained from analysis A. To maintain the observed rate of attrition of tagged fish in the NSW

Table 10

Estimates of parameters and their standard errors (SE) for different reporting rates, resulting from fitting the SE model (analysis B: unconstrained Ms) to data from experiments 2 and 4 (Table 5). All mortality and movement parameters are in units per year. Estimates were not available for reporting rates less than 0.8 because of a boundary condition on the M_1 estimate.

	Reporting rate					
	1.0		0.9		0.8	
Parameter	Estimate	SE	Estimate	SE	Estimate	SE
M_1	0.2810	0.2446	0.1612	0.5384	0.3555 E−1	0.6471 E−1
M_2	0.1158 E+1	0.3541	0.1207 E+1	0.7392	0.1170 E+1	0.8124 E−1
M_3	0.1909	0.5157 E−1	0.2064	0.9149 E−1	0.2043	0.2620 E−1
q_1	0.2032	0.4287 E−2	0.2253	0.4768 E−2	0.2526	0.5369 E−2
q_2	0.9334 E−2	0.6819 E−3	0.1020 E−1	0.7734 E−3	0.1146 E−1	0.8439 E−3
q_3	0.4623 E−3	0.9814 E−3	0.4932 E−3	0.2231 E−2	0.4590 E−3	0.1241 E−3
T_{12}	0.5384	0.6562 E−1	0.5652	0.6965 E−1	0.5655	0.7271 E−1
T_{13}	0.1094	0.2329	0.1211	0.5424	0.1447	0.3296 E−1
T_{21}	0.4508 E−1	0.4324 E−2	0.4364 E−1	0.4265 E−2	0.4354 E−1	0.4232 E−2
T_{23}	0.1636	0.3466	0.1614	0.7162	0.1913	0.4084 E−1

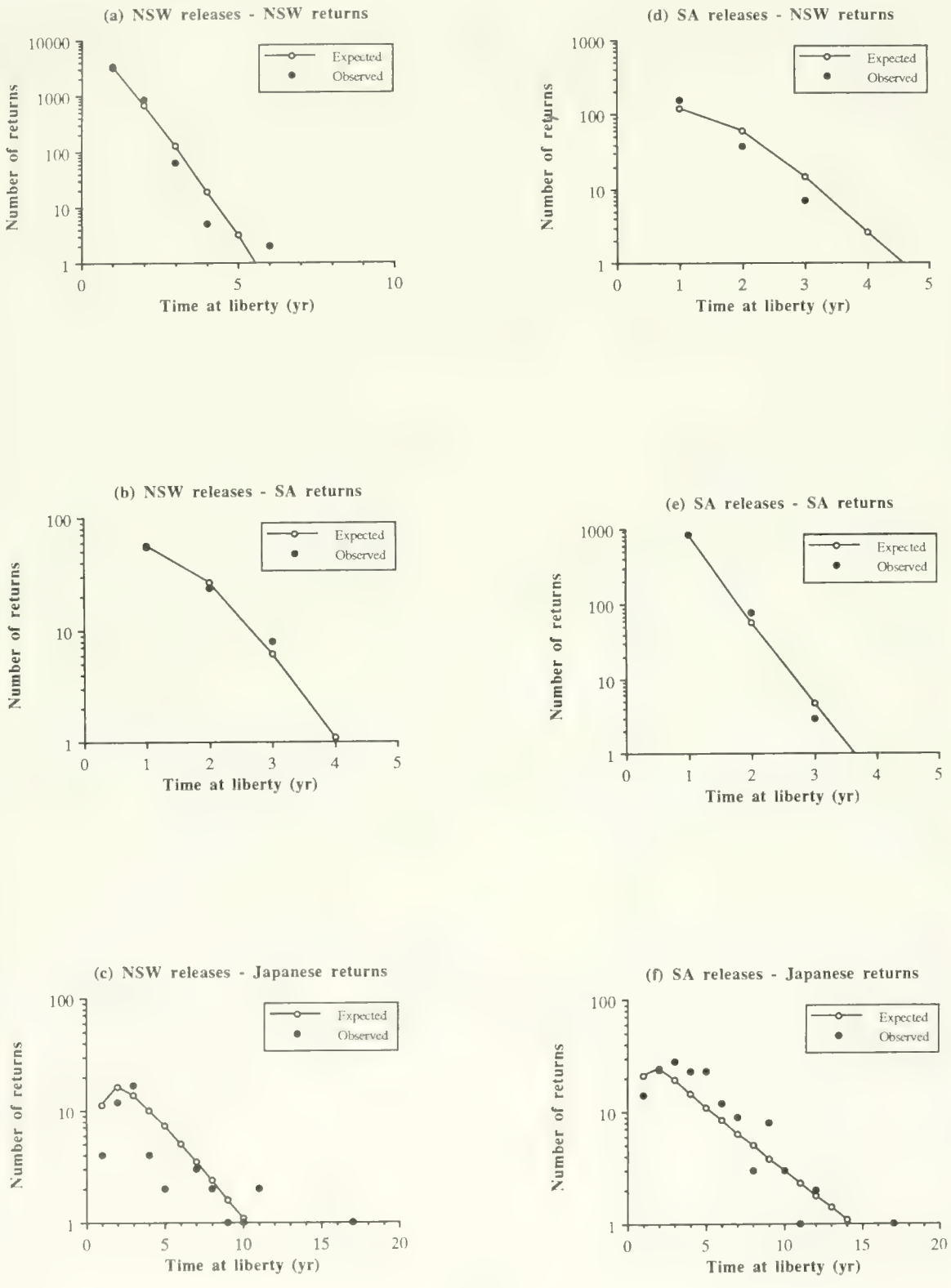


Figure 2

Plots of observed and expected numbers of returns of tagged southern bluefin tuna for analysis A. Expected numbers of returns were calculated on the basis of the constrained-M fit using the SE method.

Table 11

Correlation matrix for parameter estimates resulting from fitting the SE model (analysis B: unconstrained Ms) to data from experiments 2 and 4 (Table 10) for a reporting rate of 1.0. The matrix was estimated by the inverse-Hessian method (Bard 1974).

Parameter	M_1	M_2	M_3	q_1	q_2	q_3	T_{12}	T_{21}	T_{13}	T_{23}
M_1	1.00									
M_2	0.94	1.00								
M_3	−0.85	−0.87	1.00							
q_1	−0.01	−0.02	0.01	1.00						
q_2	0.10	0.14	−0.07	−0.07	1.00					
q_3	0.97	0.98	−0.86	−0.01	0.03	1.00				
T_{12}	−0.31	−0.05	0.07	0.13	−0.29	−0.07	1.00			
T_{21}	0.00	0.01	−0.03	−0.08	0.35	0.00	0.03	1.00		
T_{13}	−0.97	−0.98	0.87	0.01	−0.03	−0.99	0.06	−0.00	1.00	
T_{23}	−0.96	−0.98	0.88	0.01	−0.02	−0.99	0.07	0.01	0.99	1.00

fishery, a compensatory increase in T_{12} is observed. The estimate of M_2 is again relatively high (1.16/year) while the estimate of M_3 compares closely with that obtained from the unconstrained-M fit in analysis A. Recall that releases into fishery 2 (SA/WA) for analysis B were made some distance away from the commercial fishery operating at the time. This could explain the much lower estimate of q_2, and as a result, fishing mortality (~0.04/year). Similarly, the smaller estimates of movement from WA/SA into the NSW and Japanese fisheries is likely to be due to the fish being released further away from those fisheries.

The standard errors of the estimates that were obtained for the unconstrained-M fit are somewhat less than the equivalent values for analysis A, but are nonetheless far too high for the estimates to be considered reliable. The correlation matrix (Table 11) reveals a similar pattern of correlation among the parameters as was observed for analysis A.

It was not possible to obtain estimates of standard errors for reporting rates less than 0.8 because of a boundary condition with respect to the M_1 estimate, which approached zero for low reporting rates (the Hessian matrix could not be inverted because it was not positive definite). This also indicates that the parameter estimates obtained from this data set for reporting rates less than 0.8 are not the maximum likelihood estimates and therefore cannot be considered reliable.

A constrained-M fit resulted in much smaller standard errors, changes in parameter estimates consistent with analysis A (Table 12) and much lower correlation among parameters (Table 13). A likelihood ratio test (assuming $R = 1.0$) again indicated that the unconstrained-M fit is significantly better than the constrained-M fit ($P < 0.01$). However acceptance of the more complex model cannot be justified in view of the large standard errors and correlations among the parameter estimates. Plots of observed and expected numbers of returns (Fig. 3) indicate a good fit of the constrained-M model to the data.

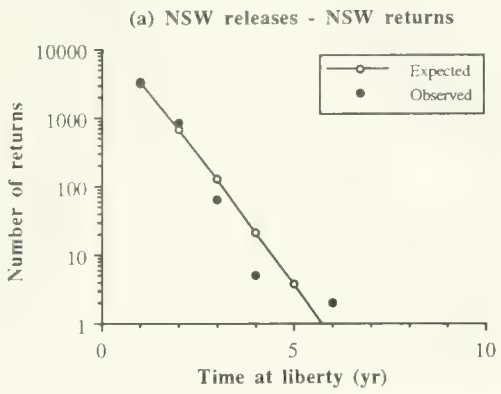
Simulation results

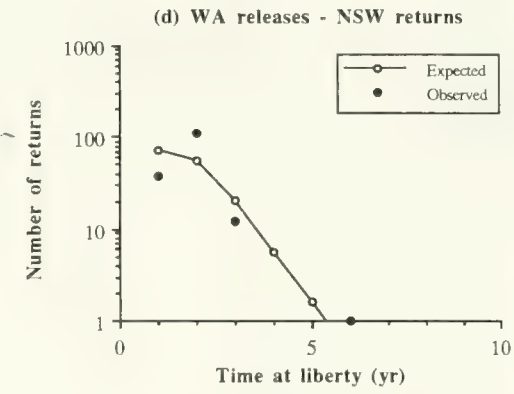
Simulated data sets were analysed in order to test the performance of the HSH and SE models. The simulations were designed to produce data sets identical in their characteristics to experiment 2 and 3 (analysis A), with the exception that tag shedding and non-reporting were not considered. Two sets of simulations were performed: type 1 simulations used the results of the analysis A unconstrained-M fit as input parameters; type 2 simulations used the results of the analysis A constrained-M fit as input parameters. Thirty data sets were produced for each simulation. Type 1 simulated data were analysed by the SE model using both unconstrained-M and constrained-M fits. Type 2 simulated data were analysed using the SE model constrained-M fits and the HSH model in order to provide a basic comparison between the two models.

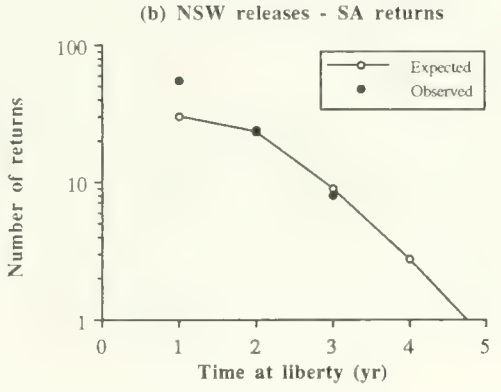
Parameter estimate means and their standard deviations for type 1 simulations are given in Table 14 for the unconstrained-M fits and Table 15 for the constrained-M fits. These results indicate that (i) the unconstrained-M fit provides unbiased estimates of all parameters, and (ii) the constrained-M fit to simulated data behaves in an identical fashion to similar fits to real data in terms of the changes in the estimates of q_3, T_{13}, and T_{23}. Moreover, the accurate recovery of parameters input to the simulation model demonstrates the soundness of the SE method as applied to southern bluefin tuna tagging data.

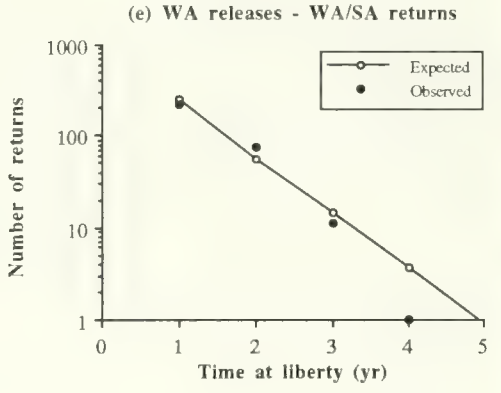
Table 16 provides a direct comparison of parameter estimates obtained by fitting the HSH and SE models to type 2 simulated data. The results indicate that the HSH model considerably overestimates M. The mean estimates from simulated experiments 2 and 3 and the mean estimate based on pooled data are almost identical (0.42–0.43/year) and are nearly double the value of M input to the simulation model. The SE model, on the other hand, is able to accurately retrieve the parameters input to the simulation model. This result casts considerable doubt on the estimates of M for southern bluefin tuna obtained using the HSH model.

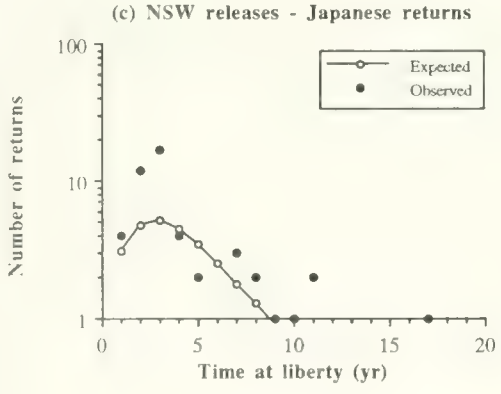
The reason for the biased estimates of M obtained using the HSH model appears to lie in the very low











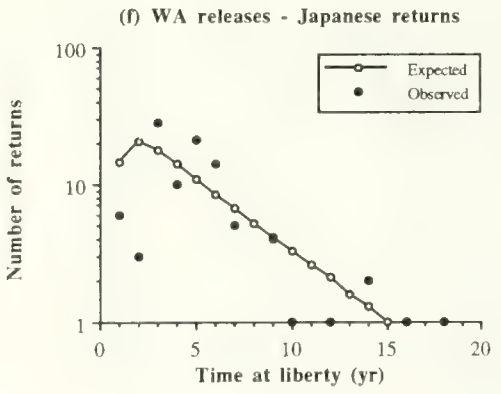


Figure 3

Plots of observed and expected numbers of returns of tagged southern bluefin tuna for analysis B. Expected numbers of returns were calculated on the basis of the constrained-M fit using the SE method.

Table 12

Estimates of parameters and their standard errors (SE) for different reporting rates, resulting from fitting the SE model (analysis B: constrained Ms) to data from experiments 2 and 4 (Table 4). All mortality and movement parameters are in units per year.

	Reporting rate					
	1.0		0.9		0.8	
Parameter	Estimate	SE	Estimate	SE	Estimate	SE
M	0.1997	0.2409 E−1	0.1902	0.2312 E−1	0.1775	0.2184 E−1
q_1	0.2034	0.4277 E−2	0.2253	0.4728 E−2	0.2524	0.5292 E−1
q_2	0.9575 E−2	0.6858 E−3	0.1076 E−1	0.7666 E−3	0.1221 E−1	0.8666 E−3
q_3	0.8078 E−4	0.1169 E−4	0.8863 E−4	0.1270 E−4	0.9765 E−4	0.1379 E−4
T_{12}	0.4123	0.4112 E−1	0.3837	0.3748 E−1	0.3475	0.3313 E−1
T_{13}	0.3163	0.4327 E−1	0.2748	0.3907 E−1	0.2249	0.3385 E−1
T_{21}	0.4429 E−1	0.4230 E−2	0.4470 E−1	0.4258 E−2	0.4489 E−1	0.4262 E−2
T_{23}	0.1082 E+1	0.7458 E−1	0.1087 E+1	0.7400 E−1	0.1083 E+1	0.7267 E−1
	0.7		0.6		0.5	
	Estimate	SE	Estimate	SE	Estimate	SE
M	0.1575	0.2000 E−1	0.1215	0.1753 E−1	0.6137 E−1	0.1493 E−1
q_1	0.2857	0.5968 E−2	0.3272	0.6776 E−2	0.3746	0.7561 E−2
q_2	0.1422 E−1	0.1004 E−2	0.1701 E−1	0.1195 E−2	0.2106 E−1	0.1471 E−2
q_3	0.1055 E−3	0.1460 E−4	0.1073 E−3	0.1461 E−4	0.9352 E−4	0.1292 E−4
T_{12}	0.2994	0.2796 E−1	0.2389	0.2214 E−1	0.1694	0.1618 E−1
T_{13}	0.1713	0.2755 E−1	0.1175	0.2036 E−1	0.7254 E−1	0.1342 E−1
T_{21}	0.4534 E−1	0.4288 E−2	0.4643 E−1	0.4376 E−2	0.4936 E−1	0.4620 E−2
T_{23}	0.1091 E+1	0.7116 E−1	0.1109 E+1	0.6899 E−1	0.1151 E+1	0.6650 E−1

apparent fishing mortality inflicted upon the tagged population by the Japanese fishery. Recall that one of the assumptions of the HSH method is that fishing mortality is maintained on the tagged population until completion of the experiment. However, as F approaches zero for older age classes, overestimates of M result from this model. To confirm this, the type 2 simulations were rerun, with the only change being an increased input value of q_3 such that F for the Japanese fishery was increased to 0.2/year (the value derived from real data and previously used in the simulations involving the HSH method was 0.007/year). Under these conditions, the HSH model provided mean estimates of M of 0.24/year for the analysis of experiment 2, experiment 3, and the two experiments pooled. This agrees well with the value for M of 0.23/year input to the simulation model.

Table 13

Correlation matrix for parameter estimates resulting from fitting the SE model (analysis B: constrained Ms) to data from experiments 2 and 4 (Table 12) for a reporting rate of 1.0. The matrix was estimated by the inverse-Hessian method (Bard 1974).

Parameter	M	q_1	q_2	q_3	T_{12}	T_{21}	T_{13}	T_{23}
M	1.00							
q_1	0.02	1.00						
q_2	−0.07	−0.06	1.00					
q_3	0.81	0.02	−0.11	1.00				
T_{12}	−0.11	0.15	−0.21	−0.01	1.00			
T_{21}	−0.06	−0.09	0.36	−0.08	0.02	1.00		
T_{13}	−0.44	0.06	0.20	−0.43	−0.75	−0.05	1.00	
T_{23}	−0.45	−0.07	0.62	−0.41	0.07	0.48	0.16	1.00

Discussion

This paper represents the first specific attempt to estimate the southern bluefin tuna natural mortality rate from tagging data. The simulation results confirm that the method of Hearn et al. (1987) will overestimate M substantially when the apparent fishing mortality inflicted on the tagged population in the latter part of the experiment is very low. Also, the sensitivity of the M estimates to the tag-shedding model adopted makes interpretation of the results difficult, particularly as it was demonstrated by Hampton and Kirkwood (1990) that long-term shedding rates are very uncertain.

Table 14

Mean parameter estimates and their standard deviations (SD) resulting from the analysis of 30 sets of simulated data having identical characteristics to real data from experiments 2 and 3, using the SE model (unconstrained Ms). The parameters input to the simulation ("real" values) are listed separately for comparison. Simulated tag release numbers were N_{01} = 9513 and N_{02} = 7328.

Parameter	"Real" value	Mean	SD
M_1	0.71	0.69	0.016
M_2	1.49	1.55	0.087
M_3	0.20	0.20	0.018
q_1	0.20	0.21	0.0047
q_2	0.086	0.086	0.0040
q_3	0.00061	0.00067	0.000085
T_{12}	0.012	0.12	0.0099
T_{21}	0.017	0.18	0.014
T_{13}	0.097	0.11	0.011
T_{23}	0.57	0.53	0.067

Table 15

Mean parameter estimates and their standard deviations (SD) resulting from the analysis of 30 sets of simulated data having identical characteristics to real data from experiments 2 and 3, using the SE model (constrained Ms). The parameters input to the simulation ("real" values) are listed separately for comparison. Simulated tag release numbers were N_{01} = 9513 and N_{02} = 7328.

Parameter	"Real" value	Mean	SE
M_1	0.71		
M_2	1.49	0.23	0.016
M_3	0.20		
q_1	0.20	0.20	0.0044
q_2	0.086	0.087	0.0037
q_3	0.00061	0.00017	0.000018
T_{12}	0.012	0.12	0.015
T_{21}	0.017	0.17	0.014
T_{13}	0.097	0.51	0.029
T_{23}	0.57	1.86	0.088

Table 16

A comparison of mean parameter estimates and their standard deviations (SD) resulting from the analysis of 30 sets of simulated data having identical characteristics to real data from experiments 2 and 3, using the HSH and SE models (constrained Ms). The parameters input to the simulation ("real" values) are listed separately for comparison. Simulated tag release numbers were N_{01} = 9513 and N_{02} = 7328.

Parameter	"Real" value	Mean	SD
HSH model			
M (experiment 2)	0.23	0.42	0.023
M (experiment 3)	0.23	0.43	0.031
M (pooled data)	0.23	0.43	0.015
SE model			
M	0.23	0.23	0.016
q_1	0.20	0.20	0.0045
q_2	0.086	0.085	0.0043
q_3	0.00016	0.00016	0.000017
T_{12}	0.12	0.12	0.014
T_{21}	0.17	0.17	0.015
T_{13}	0.57	0.58	0.027
T_{23}	1.85	1.80	0.066

The development of a population dynamics model for tagged southern bluefin that incorporates movement between the NSW and SA/WA fisheries and offshore movement into the Japanese longline fishery, as well as natural mortality and fishery-specific catchability, appears to overcome these difficulties. Although the unconstrained-M version of the model could not provide useful parameter estimates because of high parameter correlation, accurate estimates were obtained by assuming that the natural mortality rate was the same in all fisheries, thus reducing the number of parameters to be estimated by two. For a large highly-mobile apex predator, this may not be an unreasonable assumption. However, this simplification of the model was not achieved without a small, though significant, loss in likelihood of the data.

The substantial differences in some of the parameter estimates produced by the unconstrained-M and constrained-M versions of the model simply mean that the observed data could have been produced in a number of alternative and similarly likely ways. It is unlikely that M could vary amongst the three fisheries as much as was suggested by the unconstrained-M estimates in analysis A. It is noteworthy, however, that the estimate of M_3 was similar for both analyses and also compared well with the constrained-M estimates.

Compliance with model assumptions is usually difficult to assess, and this case is no exception. Tag-shedding was incorporated into both models used; therefore, in theory, the tag-shedding assumption was satisfied. In practice, the estimated shedding rates are very uncertain, particularly for the older recaptures. It would be desirable in the future to develop a method whereby uncertainties in tag-shedding rates were reflected in the standard errors of the estimated mortality and movement parameters. This might be achieved by the simultaneous estimation of shedding, mortality, and movement rates from double-tagging data.

There are no data available on which the calculation of reporting rates could be based; all estimations were therefore carried out for a range of reporting rates. Fortunately, the M estimates were largely insensitive to assumed reporting rates greater than about 0.7 in the case of the constrained-M estimates. It is worth

noting that the high recovery rate of tags released in NSW would suggest a high reporting rate in that fishery at least.

The few data available suggest that mortality associated with tagging southern bluefin tuna is slight. Animals have been reported to survive in good condition for 80 hours in a live bait tank after having been tagged (Robins 1963). Furthermore, Hynd and Lucas (1974) considered that the behavior of the fish immediately following tagging was consistent with slight or no tagging mortality. Personal observations in the field also support this hypothesis. If tagging mortality occurred and was immediate or nearly so, its effect on the parameter estimates would be slight and identical to that of non-reporting. If there was significant, continuous tag-induced mortality (which is unlikely), M would tend to be overestimated by both methods used in this paper.

The assumption of constant M has not been tested in this paper, but the possibility that a model with age-dependent M might provide a better fit to the tagging data should not be ruled out. Generalization of the SE model in this regard would be possible and may yield useful results, although similar estimation problems to those of the unconstrained-M fits might occur.

The final assumption concerns equal vulnerability of the tagged and untagged populations and is possibly the most difficult with which to comply. Strict compliance would require that either the fishing effort is distributed randomly with respect to both the tagged and untagged populations, or that the tagged population is distributed randomly with respect to the untagged population. The first possibility is seldom seen in practice because fishermen tend to direct their effort in areas of high fish concentration. If these areas happen to coincide with the areas of tag release (as is often the case), the number of recaptures during the first period after release may be larger than expected. This would result in overestimates of M and other components of tag attrition using the SE method. Similarly, the second possibility is not usually feasible, as it would require tagged fish to be released over a wide area within a short space of time. However, for highly mobile tunas such as southern bluefin, mixing is likely to be rapid, thus lessening the problem to a large extent. In the case of the NSW fishery, many tagged fish were released prior to the fishing season, which would tend to enhance mixing. Division of the Australian fishery into two components also helps compliance with this assumption. From this point of view, even further stratification would have been desirable; however, this would greatly complicate the algebra and probably result in statistical problems with parameter estimation.

The fishing mortality inflicted on tagged southern bluefin by the Japanese fishery would appear to be slight (<0.06/year for assumed reporting rates >0.5) compared with values of 0.15–0.40/year obtained from cohort analysis (Hampton 1989). This discrepancy could result because southern bluefin migrating through Australian coastal waters are subsequently somewhat less available to the longline fishery than the population in general. Such differential availability to surface and longline fisheries has been noted for other tuna stocks, e.g., populations of yellowfin tuna in the Pacific (Lenarz and Zweifel 1979, Suzuki 1988) and Atlantic Oceans (Fonteneau 1986, Suzuki 1988). While not necessarily affecting the estimates of M, caution should be exercised in the interpretation of estimates of fishing mortality derived from these tagging experiments.

The results of estimations using the SE method were consistent in suggesting a value of M, in the Japanese fishery at least, of approximately 0.2/year. There was little information in the data regarding M in the Australian surface fisheries; however, a value similar to the above is not an unreasonable, if tentative, conclusion. Analysis of more recent tagging experiments may, in due course, help to resolve this question.

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Abstract.—The relationship between length and age of larval and juvenile shortbelly rockfish *Sebastes jordani*, determined from otolith microstructure, is complex. Models that assume size increases smoothly with age may not accurately describe growth in young-of-the-year rockfish. A segmented (piece-wise linear) regression model relating somatic and otolith size was used to back-calculate body length-at-age. The segments of this model coincide with different growth stanzas, which are separated by distinct life-history transitions. The composite function of this model, and a Gompertz curve relating otolith size and age, yielded a good fit to the back-calculated standard length-at-age data. Comparison of back-calculated with actual growth showed no evidence of size-selective mortality. The change in body length, as the number of otolith increments increased, was equal to the observed increase in length per day of a sequentially sampled cohort, validating the daily periodicity of the increments.

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Dynamics of Growth in the Early Life History of Shortbelly Rockfish *Sebastes jordani*

Thomas E. Laidig
Stephen Ralston
James R. Bence

Tiburon Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
3150 Paradise Drive, Tiburon, California 94920

The abundance of young-of-the-year fish, and ultimately the number that reach maturity, varies greatly among years. Much of this variation is unrelated to the size of the spawning stock, and understanding its causes remains a central focus of fisheries research (e.g., Hjort 1914, Sissenwine 1984, Rothschild 1986, Hollowed et al. 1987, Sinclair 1988). Mortality agents, such as starvation (Hjort 1914, Lasker 1975 and 1978, Houde 1977 and 1978, Theilacker 1978 and 1981, Grover and Olla 1986) and predation (Hunter 1981, Hunter and Kimbrell 1980, Sissenwine 1984, Bailey and Houde 1989), can operate strongly during early stages, and it is clear that mortality rates of young fish are higher than those experienced by older fish (Miller et al. 1988). Interannual variation in year-class strength can depend upon the rate of growth early in life (Houde 1987 and 1989, Underwood and Fairweather 1989). Under most conditions, the more rapidly fish grow through early, high-risk stages, the fewer die; small changes in growth rate can thus lead to a major change in recruitment (Houde 1987). Knowledge of the processes affecting growth during the early life history may help predict the occurrence of strong year-classes.

Numerous mathematical models have been developed to describe the growth process, including the Gompertz, von Bertalanffy, logistic, and exponential functions (Ricker 1979). Although these models usually perform well on adult stages, they commonly falter in predicting growth during the first few weeks of life. For example, Phillips (1964) used a von Bertalanffy function to model growth of shortbelly rockfish *Sebastes jordani*. The model predicted growth of adults well, but its accuracy deteriorated for young-of-the-year fish. Because somatic growth during early stages can be affected by abrupt physiological changes (e.g., flexion, juvenile transformation, and settlement), models that predict growth during this period should reflect (or describe) this complexity (Ricker 1979).

Rockfish (*Sebastes* spp.) are an important component of the west coast groundfish fishery (PFMC 1989). Growth rates of young rockfish have been estimated from linear models relating length to age (Boehlert 1981, Boehlert and Yoklavich 1983, Penney and Evans 1985, Haldorson and Richards 1987, Woodbury and Ralston 1991). Because most of these studies examined a narrow range of ages, linear models fit the data adequately. Although Penney and Evans (1985) showed that a linear model explained much of the variation in length during larval and juvenile stages of redfish, back-calculated growth rates varied systematically with age; growth rate was relatively slow for young larvae, more rapid

for older larvae, and relatively slow again for juveniles. This suggests that it is possible to improve upon the linear model and provide a more accurate description of growth over the entire range of ages.

Since Pannella (1971) first discovered daily growth increments in otoliths, many researchers have used these microstructural features to study fish growth (see reviews in Campana and Neilson 1985, Jones 1986). By measuring the widths of daily increments within the otolith, and defining the relationship between standard length and otolith radius, one can back-calculate the somatic length of fish at any given age. This approach provides a powerful tool for estimating growth rates (e.g., Thorrold and Williams 1989). In this study, we used otolith microstructure to back-calculate the growth of larval and juvenile shortbelly rockfish *Sebastes jordani*. To do this we (1) determined when daily increments begin to form, (2) validated the daily periodicity of the increments, (3) developed a growth model for back-calculation, and (4) assessed the effects of size-selective mortality on back-calculated estimates of growth.

Table 1

Haul and collection data gathered during this study. On the first three cruises, larvae only were collected; on the May–June cruise, both larvae and juveniles were collected.

Dates (1989)	Research vessel	No. hauls	No. collected	No. aged
01 Feb.	RV *Ed Rickettes*	7	191	153
18 Feb.	RV *David Starr Jordan*	2	31	31
06 March	RV *Ed Ricketts*	5	27	10
14 May–13 June	RV *David Starr Jordan*	168	1262	55

Methods

Field collections

Larval and juvenile shortbelly rockfish were collected on four cruises between 1 February and 13 June 1989 (Table 1). All sampling was conducted along the central California coast from Cypress Pt. (Monterey Co.) to Pt. Reyes (Marin Co.). Larval samples were collected with oblique tows to maximum depths of 50–200 m, and were towed at depth for 30 seconds, at an approximate ship speed of one knot. Larval samples were collected with a 1 m plankton net (0.505 mm mesh) or, for the 18 February cruise, a 2×2 m Isaacs-Kidd trawl (2 mm mesh). For further information on larval hauls, see Appendix A. Larvae were sorted and placed in 80% ethanol. Juvenile samples were collected with a 26× 26 m midwater trawl (0.945 cm mesh codend liner), towed horizontally at depth for 15 minutes at a speed of approximately one knot. Sampling for the juvenile survey was at fixed stations spread throughout the study area, with target depths of 10, 30, and 100 m, but with most samples taken at the standard depth of 30 m. Juvenile rockfish were removed from hauls and immediately frozen. For further details on procedures for the juvenile survey, see Wyllie Echeverria et al. (1990).

To determine when daily otolith increments begin to form, gestating larvae (rockfish are viviparous livebearers) were collected and their otoliths examined. Adult female rockfish were collected during the May–June survey and from commercial fishermen at Fort Bragg, California in May. Preextrusion larvae were removed and placed in 80% alcohol for later examination.

Laboratory procedures

The stage of development of the gestating larvae was determined by morphology and pigmentation (Moser et al. 1977). Larvae from four females (two from the May–June cruise and two collected from commercial fishermen in May) were found to be in an advanced stage of development and were used for further analysis.

The standard length (SL) of all larvae and juveniles was measured to the nearest 0.1 mm. Ages were determined for juveniles spanning the entire size range collected and for all planktonic larvae. Sagittae were removed from each fish and affixed whole to slides with a drop of clear fingernail polish. Intact otoliths from larvae (<20 mm) had discernable growth increments with no further preparation. For fish with SL >20 mm, otoliths were sanded in the sagittal plane with 400-grit sandpaper until the nucleus became visible. Concentrated HCl was used to etch the otoliths until growth increments were easily discernable.

All otoliths were viewed at 600–1250× magnification with a compound microscope equipped with a video camera and monitor. Only fish with a dark check mark that clearly encircled the primordium were used in our analysis of growth (see also Penney and Evans 1985). Fish with this mark and no additional increments were given a nominal age of zero. Increments were counted from this mark to the most distal point along the postrostral growth axis. We used a digitizer to record the exact position of each increment; otolith radius (OR) was measured to the nearest 0.1 μm.

Validation

To validate that the increments were formed daily, we only considered samples collected during the May–June survey, because it was the only multiple-day cruise. From the data we identified a well-defined, temporally discrete cohort, and estimated the average change in length of individuals over the duration of the cruise. We compared this rate with the rate of change in length with nominal age from otoliths.

We identified a temporally discrete cohort as follows. Using the 55 aged fish (mainly juveniles) from the May–June cruise, and assuming that the number of increments approximated age in days after extrusion, we linearly regressed age on SL. From the resulting regression equation, we estimated the ages of all juveniles caught (all specimens were measured, but only a subsample of 55 fish from this cruise was aged). By subtracting estimates of age from known dates of capture (measured from the beginning of the year), we estimated the dates when the dark check mark formed for all fish sampled. A plot of frequency of occurrence against estimated dates of check mark deposition was used to identify the cohort. We stress that this procedure was used only to identify the cohort for further consideration. The rate of change in length-per-unit-time for fish sampled from the cohort was found by calculating the rate at which the lengths of captured individuals changed over the course of the 30 day cruise.

Data analysis

Initial exploratory model development involved fitting a number of equations (by least squares) to the data to characterize two functional relationships: OR = f(age) and SL = g(OR). For the former, we used not only the radius of the otolith at the time of collection (terminal OR), but also back-calculated radii measured at earlier ages. Due to the serial correlation present in these data (multiple observations of OR-at-age from the same fish), we used the grouped jackknife technique (Miller 1974) to estimate standard errors of the parameters. In contrast, we used only terminal values of OR and SL when fitting the latter relationship. Once known, the composition of these two functions $\{f^{o}g\}$ defined explicitly the dependence of SL on age, i.e., $\widehat{SL} = g(f(age))$. This procedure provided a better description of the age-length relationship than did the more usual approach of fitting a growth model to back-calculated SL-at-age data, even when complex formulations were tried (e.g., the two-stage Gompertz function suggested by Zweifel and Lasker 1976).

A single-stage Gompertz growth equation (Ricker 1979) provided a good description of otolith growth. The model has three parameters (OR_0, k, and g) and can be expressed as:

$$OR = OR_0 \cdot \exp\{k \cdot [1 - \exp(-g \cdot age)]\}.$$

Our data showed increasing variance in OR with increasing age, so the data and the equation were logarithmically transformed prior to fitting (Zweifel and Lasker 1976).

To regress SL on OR, we developed a model consisting of four linear segments, each describing a different growth stanza (see Appendix B for details). Before selecting this segmented model, we first considered, and then discarded due to lack of fit, a number of continuous models, including the simple two-parameter linear model, the Gompertz function, and three-parameter power and exponential models with separate Y-intercept terms.

Once we had established a relationship between SL and OR, we used this relationship to back-calculate SL at ages younger than the terminal age-at-capture. We used the "body-size proportional" method described by Francis (1990) in our back-calculations, in which the length at age i (some age younger than c, the age of collection) for fish j (SL_{ij}) is given by:

$$SL_{ij} = g(OR_{ij}) \cdot (SL_{cj}/g(OR_{cj})),$$

where, as above, $g(\cdot)$ is the regression equation we developed to predict expected SL from OR, and SL_{cj} is the measured length of fish j at the time of capture. Note that this method corrects for the deviation between the length predicted by the regression model and actual length at the time of capture. The well-known Fraser-Lee method, which also takes into account actual length of an individual at the time of capture, is inappropriate here because of the non-linear relationship between SL and OR (Campana 1990, Francis 1990). The fit of $\widehat{SL} = g(f(age))$ to the "observed" back-calculated estimates of SL_{ij} was then evaluated by examining a plot of the residuals ($SL_{ij} - \widehat{SL}$).

Results

We measured SL of 1511 larval and juvenile shortbelly rockfish. Ages were determined for 249 fish that ranged in size from 4.5 to 74.5 mm SL. Of these, 194 (4.5–15.2 mm SL) were from the three single-day cruises and 55 (14.6–74.5 mm) were from the May–June cruise (Table 1).

None of the gestating preextrusion larvae that we examined possessed the dark check mark that we used as the starting point for increment counts. Because of this, and the presence of increments in most of the

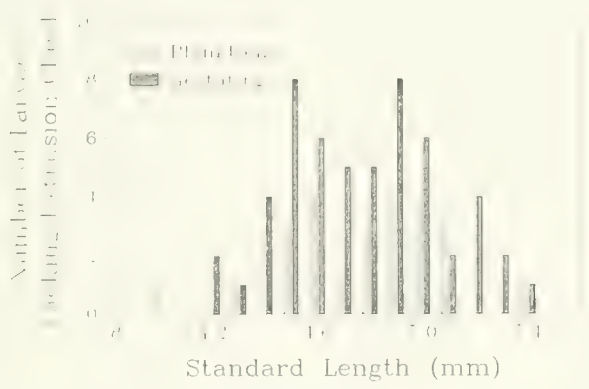

Figure 1
Size distributions of fully developed gestating (n 54) and planktonic (n 25) larvae of shortbelly rockfish lacking the extrusion check.

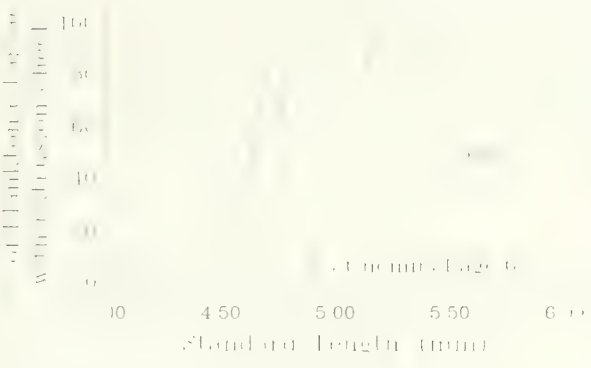

Figure 2
Change with length in the percentage of planktonic shortbelly rockfish larvae (n 25) exhibiting the extrusion check.

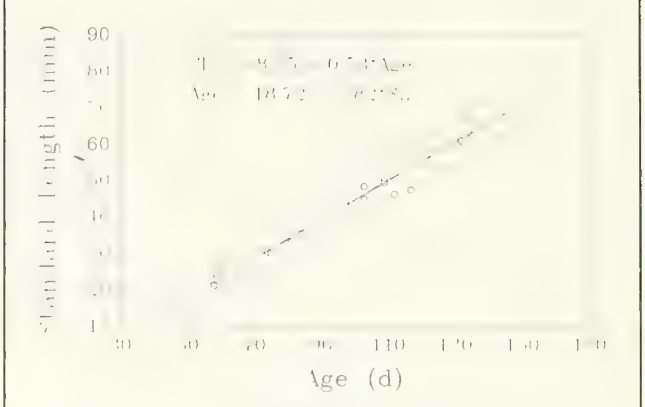

Figure 3
Least-squares regressions relating standard length and age for juvenile shortbelly rockfish collected during the May–June survey off central California, 1989.

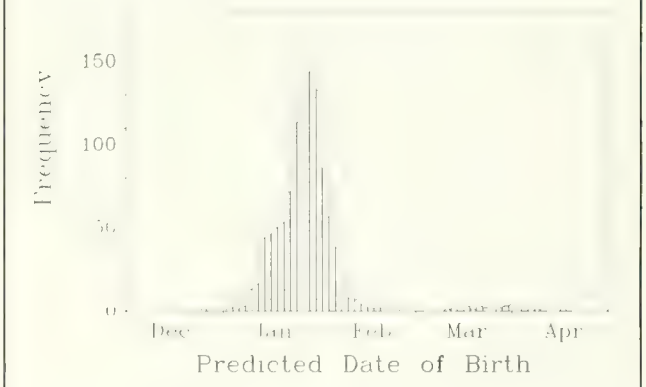

Figure 4
Frequency distribution of birthdates (date of extrusion check) for all shortbelly rockfish caught during the May-June survey off central California, 1989. Note the existence of a small but discrete second cohort spawned in March and April.

smallest planktonic larvae, we believe this mark was formed at, or shortly after, extrusion. The size distribution of the few planktonic larvae that lacked this feature (henceforth called the extrusion check) was similar to the size distribution of full-term, gestating larvae (Fig. 1). Thus, shortbelly rockfish do not appear to grow substantially from the time of extrusion to the time the extrusion check is formed. Likewise, all planktonic larvae greater than 5.5 mm in length had an extrusion check and more than 50% had the extrusion check, at a size of 4.7 mm (Fig. 2). The average size of the full-term gestating larvae we measured was 4.7 mm, and we take this as an estimate of the size-at-extrusion, which is independent of our growth models.

Validation

We compared how the mean SL of fish in a cohort changed over a 30-day period, with the growth rate estimated from a regression of SL on nominal age determined independently by examining otoliths. For the 55 fish we aged from the extended May–June cruise, a linear relationship existed between assumed daily age and SL, with a slope of 1.82 days/mm (SE 0.0484) and an r^2 of 0.963 (Fig. 3). The distribution of estimated birthdates for all juveniles caught during the cruise (N 1262) contained a small secondary mode (N 25) in March and April (Fig. 4). In our primary analysis, we considered only those fish with birthdates occurring in January or February (N 1237).

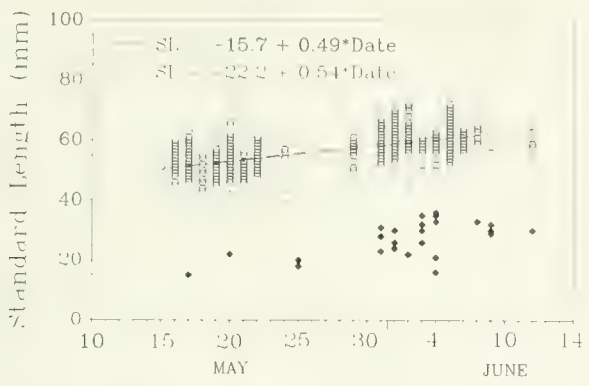

Figure 5

Regressions of standard length on calendar date of capture for all juvenile shortbelly rockfish taken during the May–June survey off central California, 1989 (solid line; r^2 0.265) and for the subset of juveniles that were extruded during the primary January–February spawn (open circles and dashed line; r^2 0.484). Diamonds represent the fish (n 25) spawned during March and April.

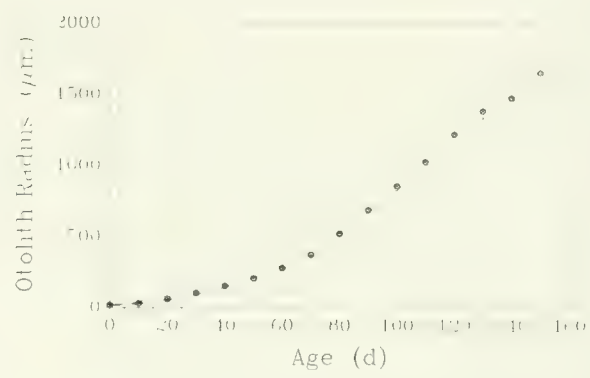

Figure 6

Predicted otolith radius as a function of age (solid line) from the Gompertz growth model (multiple observations from each specimen). Filled circles are means of the observed data at 10-day intervals, bracketed by ±2 standard errors. Note that standard errors for younger ages do not appear due to the resolution of the figure. Dashed lines enclose the range of data.

For the juveniles from the first cohort, the slope of the regression of SL on date of capture was 0.54 mm/day (SE 0.0158; Fig. 5). This compares with a slope of 0.53 mm/increment (SE 0.0140) obtained from a regression of length against the number of increments counted for the 55 aged fish (Fig. 3). Moreover, the slope of a regression of the predicted ages of the fish from the first cohort on their date of capture was 0.96 increments/day (SE 0.028). This rate is not significantly different ($P>0.05$) from the expected 1:1 correspondence between increments and days (t −1.43, df 1235).

Most of the fish from the second cohort (Fig. 4) were captured late in the May–June cruise, probably because selectivity of the net did not allow their capture at the beginning of the cruise when they were smaller. Because fish from the second cohort were smaller and were caught later in the cruise, excluding them improved the agreement between the observed rate of change in length over time and the growth rate estimated from daily otolith increments of aged fish (Fig. 3). We feel that the exclusion was warranted because of the clear separation between the cohorts (Fig. 4). In any case, relatively few fish (25 out of 1262) were excluded, and the effect on our estimated rate of change in length of the cohort was slight (~10%; Fig. 5).

Growth of the otolith

Otoliths of shortbelly rockfish grow at a generally increasing rate from birth to ~90 days in age (Fig. 6). Thereafter, there is substantially less curvature in the data. Results of fitting the Gompertz growth function to the data yielded estimates of $OR_0 = 16.00\,\mu m$ (SE 0.0374), k = 5.4223 [dimensionless] (SE 0.0235), and g = 0.01298/day (SE 0.000106), with an r^2 of 0.991. The curve (solid line in figure) fit the data well except for a minor lack of fit at about 70 days of age.

Standard length vs. otolith radius and back-calculation of length

The segmented linear model (after Bacon and Watts 1971) provided a good fit when SL was regressed on OR (Fig. 7, Table 2). There was no discernable pattern to the residuals, and the r^2 value was quite high (0.998). In addition, the model's estimate of body length at the mean otolith radius at the extrusion check (17 μm) was 4.9 mm SL; this approximated independent estimates of length-at-extrusion (5.4 mm [Moser et al. 1977], 4.0 mm [MacGregor 1986], and 4.7 mm SL [this study, Figs. 1, 2]). The intersections of the four linear segments relating SL to OR were at 38.7, 73.1, and 431.3 μm OR, and the corresponding lengths were 7.7, 8.4, and 29.9 mm SL, respectively.

Larvae were collected with two types (sizes) of nets. A possible source of bias in our results could arise from different selectivities of the nets (Somerton and Kobayashi 1989). For example, differential sampling by the nets may be responsible for the segmenting seen in Figure 7, although we do not believe this is the case. Even though, on average, the nets collected different sized fish, both types of nets captured fish in the range

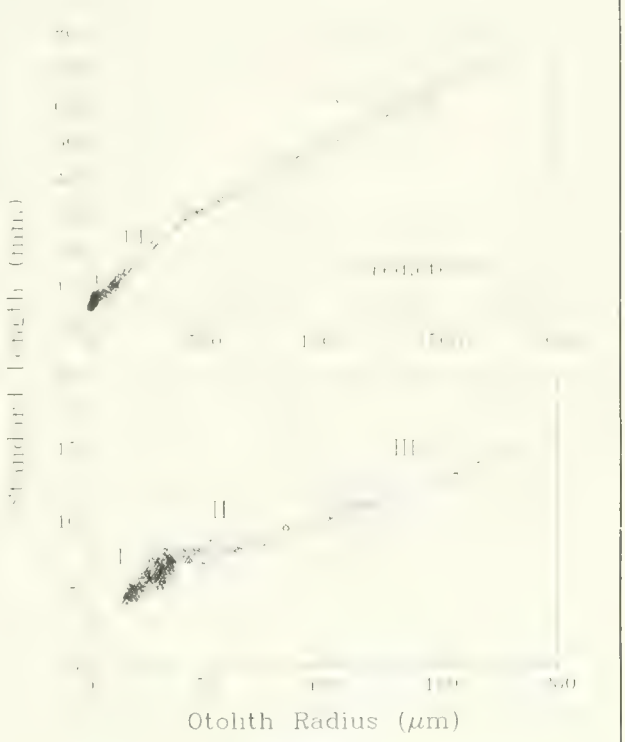

Figure 7

Plot of terminal standard length and otolith radius for all aged shortbelly rockfish (N 249). Shown is the predicted curve from the segmented model spanning the full range of data (upper panel), with Roman numerals for each of the four distinct growth stanzas. The lower panel enlarges the earliest growth stages (<200 μm OR). Circles are fish taken in Isaacs-Kidd trawls, and triangles are from plankton nets.

Table 2

Parameter estimates for the segmented regression model describing the relationship between standard length (mm) and otolith radius (OR, μm); Y-intercept (a), slopes for each segment (b_1–b_4), and intersection points of the segments (c_1–c_3) on the X (OR) axis. Note that, except for c_1–c_3, these are algebraic transformations of the actual parameters fitted by the regression procedure (see Appendix B). Estimates of length for a given OR based on the values given below ignore the smoothing described in Appendix B, but will be close approximations of the values that would be obtained using the original parameterization.

Transformed parameter	Estimate
a	2.92
b_1	0.1233
b_2	0.0219
b_3	0.0599
b_4	0.0327
c_1	38.72
c_2	73.10
c_3	431.31

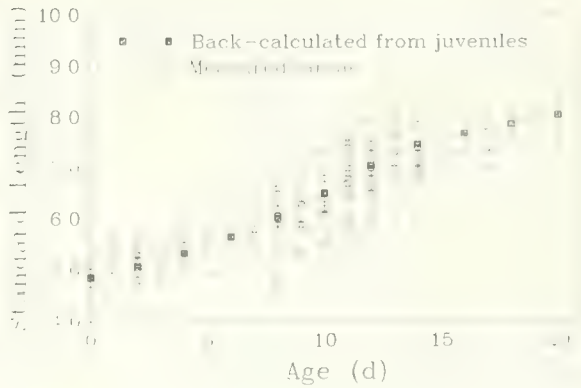

Figure 8

Scattergram of terminal standard length and age for larvae ≤20 days (open circles). Solid line depicts the back-calculated mean size-at-age (±1 SD) during the larval stage of juvenile fish (terminal age ≥60 days).

of 7.5–10.0 mm SL (lower panel of Figure 7). Within this range, the relationship of SL to OR did not differ significantly between the nets (t 0.50, df 4, $P>0.05$).

Standard length vs. age

Our back-calculation of standard length-at-age (SL_{ij}) is based on the implicit assumption that the mean back-calculated length at any particular age is similar to the mean length of fish actually captured at those earlier ages. Violation of this assumption is the so-called Rosa Lee's phenomenon (Ricker 1979), which can arise when mortality rates are size-selective and from a number of other causes, such as biased sampling. However, our data show that mean length-at-age during the first 20 days of life, back-calculated from juveniles at least 60 days old, passes through the observed values of SL and age at the time of capture for young larvae (Fig. 8). This result suggests that Rosa Lee's phenomenon is unlikely to distort our findings to any appreciable degree.

The predicted fit of the composite function [$\widehat{SL}$ = g(f(age))] to the back-calculated size data was good (Fig. 9). Note that individual fish followed their own growth trajectories, producing serial correlation in the residuals. The slight lack of fit around age = 70 days (see Figure 6) is also seen more easily in this figure.

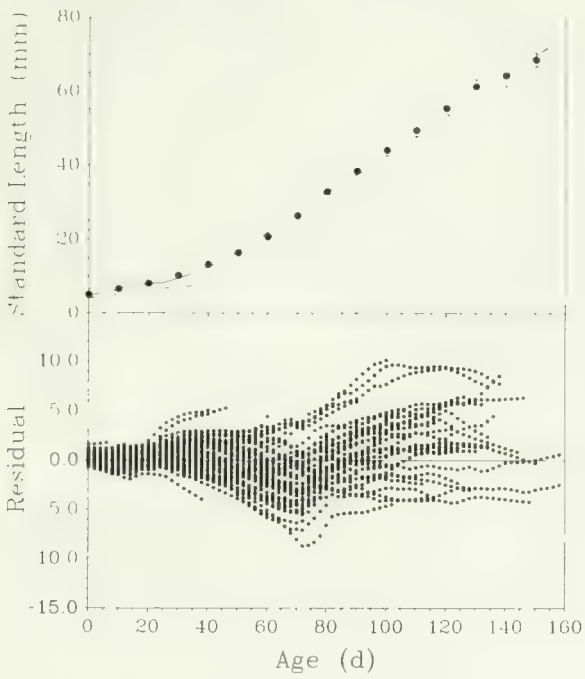

Figure 9

Relationship between back-calculated standard length and age for shortbelly rockfish. Solid line in the upper panel represents the composite function of relationships shown in Figures 6 and 7. Filled circles are means of the observed data at 10-day intervals, bracketed by ±2 standard errors. Dashed lines enclose the range of data. Residuals (observed–predicted) of the fit are shown below.

Discussion

Our goal was to develop a model that could be used to provide accurate estimates of back-calculated growth from the otolith microstructure of larval and juvenile shortbelly rockfish. A crucial assumption of the study was that the increments were formed daily. Many authors have stressed the importance of validating the daily periodicity of otolith growth increments (Jones 1986, Geffen 1987). Without validation, growth rates may be biased and their use in models of juvenile dynamics and recruitment could lead to serious errors. For validation purposes, we followed a cohort of fish through the May–June time period, measuring their progressive change in average length. We found that the rate of change in length of this cohort agreed with the estimated growth rate based on a regression of length against number of growth increments enumerated for aged fish. From this result, we conclude that the increments we counted were formed daily. It is noted, however, that the daily periodicity of these increments is validated only for the size ranges and dates observed during the extended May–June cruise, but we have no reason to assume that the increments are not daily at earlier stages of growth.

Other evidence exists that daily increments form in otoliths of *Sebastes* spp. Yoklavich and Boehlert (1987) demonstrated the daily periodicity of increment formation in otoliths of black rockfish *S. melanops* by marking the otoliths with oxytetracycline (OTC) and by autoradiography. Also, Laidig (unpubl. data) found no difference between increment counts and the number of days following a fluorescent OTC mark, verifying that the increments of brown rockfish *S. auriculatus* were interpreted correctly as daily.

Our segmented model of fish size versus otolith size, for use in back-calculating fish length, may describe significant events during the early life of *S. jordani*. The first major events following extrusion, in the early life of rockfish, are first feeding, flexion, and transformation from larva to juvenile. Moser et al. (1977) noted that shortbelly rockfish larvae undergo flexion at 8.0–10.0 mm SL. This range essentially corresponds to the size of fish in segment II. The slope of this segment was much reduced, suggesting that although fish length increases little during flexion, the otolith continues to grow. Likewise, Moser et al. (1977) found that juvenile transformation began after 27 mm SL, and we observed that the intersection of segments III and IV occurred at a length of about 30 mm SL. It is possible, of course, that the segments we have described are peculiar to the time and place that we collected the fish. For example, the slope of the fish size to otolith size relationship could have changed at specific points in time in response to altering oceanographic conditions (see also the discussion on "buffering" below). Before this type of alternative explanation can be discarded, similar SL–OR regressions need to be established in other years.

Relative to the entire organism, the sagittal otolith is a simple structure, especially during early life history. During the first 160 days of life, the sagitta develops from a spherical primordium into an oval-saucer shape. During this time a single Gompertz curve (Fig. 6) adequately described growth along one of its dimensions (i.e., the postrostral axis).

In contrast, the whole organism is morphologically and developmentally complex. Although a simple Gompertz curve, when fitted to back-calculated length (SL_{ij}) against age, resulted in a high r^2 value, an unacceptable pattern was evident in a plot of the residuals. Other authors also have found that smooth models (e.g., Gompertz and von Bertalanffy curves) did not accurately fit SL-at-age data in young-of-the-year fish (Uchiyama and Struhsaker 1981, Bailey 1982, Rosenberg and Laroche 1982, Campana 1984, Boehlert and Yoklavich 1985). Although these simplified models

often perform well on adult fish, they are sometimes unable to depict the complex growth processes characterizing the complete life history. In such cases, segmented models should be considered because they allow for life history changes and growth stanzas (Ricker 1979). For example, Watanabe et al. (1988) found that for Pacific saury *Cololabis saira*, two Gompertz curves produced a better fit to the relationship of length and the number of daily otolith increments than did a single Gompertz curve. Zweifel and Lasker (1976) showed that a two-stage Gompertz curve described the growth of anchovy *Engraulis mordax* larvae better than a simple single-stage Gompertz curve. These authors also noted that although other models had high coefficients of determination, they exhibited unacceptable predictions for small larvae. Likewise, Nishimura and Yamada (1988) found that three linear segments described the relationship between otolith length and total length for walleye pollock *Theragra chalcogramma*, and that the intersection points between segments represented changes from larval to juvenile growth and juvenile to adult growth.

Changes in growth stages or stanzas are characterized by a fundamental alteration or discontinuity in development, such as hatching, first feeding, maturation, or a change in habitat (Ricker 1979). Above we presented and reviewed some evidence for this idea from studies of fish. The concept is likely to have validity for many organisms. For example, allometric relationships for physiological rates in *Daphnia* are stage-dependent (McCauley et al. 1990).

Some authors (Reznick et al. 1989, Secor and Dean 1989) have shown that otolith growth rate is relatively insensitive to factors that cause more extensive variation in somatic growth rate (e.g., alterations in temperature and food ration). Under extreme conditions, however, daily increment deposition arrests or is otherwise seriously perturbed (Tanaka et al. 1981, Campana 1983, Neilson and Geen 1985; reviews in Campana and Neilson 1985 and Jones 1986). Nonetheless, in many instances the otolith can be considered a conservative growth structure that is buffered from environmental factors affecting somatic growth. The otolith continues to record significant events, such as transitions to other life stages, even when somatic growth is seriously impaired. Conversely, this buffering tends to obscure the otolithic record of somatic growth fluctuations arising from exogenous factors, e.g., temperature fluctuation, changes in prey density, and turbidity.

Insulation of the otolith to ambient conditions can lead to a somatic:otolith size ratio that is positively related to growth rate. Recently, Campana (1990) showed that this can lead to biased estimates of length-at-age and the appearance of Rosa Lee's phenomenon, when lengths are back-calculated by the Fraser-Lee method. He noted that this problem is unlikely to be significant when the intercept is well fixed by aging young larval fish, or through use of independent biological measurements. In our study, many of the aged fish were young larvae. In addition, the estimated length of a fish with an otolith radius equal to the mean radius at the extrusion check was in good agreement with the mean length of late-stage gestating pre-extrusion larvae. Lastly, we found no evidence that back-calculated lengths of fish captured as juveniles differed from directly measured lengths of fish captured as larvae.

Acknowledgments

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Appendix A

Detailed information on individual larval hauls.

Date	Research vessel	Gear type	Max. depth	Lat.	Long.	No. caught	No. aged
2/1	RV *Ed Ricketts*	Plankton net	150	36°48.2′	121°51.9′	22	15
2/1	"	"	150	36°48.1′	121°52.7′	42	27
2/1	"	"	100	36°47.8′	121°54.0′	27	5
2/1	"	"	100	36°47.8′	121°54.7′	48	34
2/1	"	"	200	36°47.9′	121°53.7′	32	18
2/1	"	"	80	36°48.4′	121°53.2′	36	33
2/1	"	"	100	36°48.3′	121°52.4′	13	4
2/18	RV *David Starr Jordan*	Isaacs-Kidd trawl	200	37°16.6′	122°49.1′	0	0
2/18	"	"	200	37°16.7′	122°49.0′	32	31
3/6	RV *Ed Ricketts*	Plankton net	100	36°48.2′	121°52.7′	2	1
3/6	"	"	120	36°47.8′	121°53.7′	5	4
3/6	"	"	140	36°47.2′	121°55.2′	6	6
3/6	"	"	130	36°46.4′	121°59.6′	4	4
3/6	"	"	60	36°47.2′	121°50.6′	12	8

Appendix B

Here we describe the regression model used to relate standard length to otolith radius, which consisted of a series of four linear segments, each describing a different growth stanza. We start with the following equation:

$$SL = \begin{cases} a + b_1 x \text{ for } x < c_1 \\ a + b_1 c_1 + b_2(x - c_1) \text{ for } c_1 \leq x < c_2 \\ a + b_1 c_1 + b_2(c_2 - c_1) + b_3(x - c_2) \text{ for } c_2 \leq x < c_3 \\ a + b_1 c_1 + b_2(c_2 - c_1) + b_3(c_3 - c_2) + b_4(x - c_3) \text{ for } c_3 \leq x \end{cases} \quad (1)$$

where a is the y-intercept of the first segment, x is the otolith radius, b_1, b_2, b_3, and b_4 are the slopes of the four segments, and c_1, c_2, and c_3 are the points on the x axis corresponding to the intersections. Because not all individuals would be expected to make the transition from one stanza to the next at identical sizes, it is reasonable to smooth the relationship at the segment intersections. We therefore applied the technique described by Bacon and Watts (1971) to smooth the transition between linear segments, assuming that most fish made the transition from one stanza to the next over a small size range. Specifically, we assumed that the probability that an individual fish made the transition from one stanza to the next was described by the logistic cumulative distribution function, $F(z) = 1/(1+\exp(-z))$, where $z = (x - c_i)/g$. Note that g is a constant chosen so that 95% of all transitions occur within $\pm 0.3\,\mu m$ OR of each intersection. (We assumed this rapid rate of transition rather than evaluating the transition rate from the data because preliminary analyses, with g as an estimated parameter, indicated that the density of measurements on the x axis was not sufficient to yield unique solutions. Runs with different starting parameters did not converge to the same parameter estimates.) Following Bacon and Watts (1971), we rewrote the model as:

$$SL = e + d_1(x - c_1) + d_2(x - c_1)s_1 + d_3(x - c_2)s_2 + d_4(x - c_3)s_3 \quad (2)$$

where the terms relate to equation 1 as follows:

$$s_i = 2*(F((x - c_i)/g) - 1;\ i = 1,2,3;\ g = 0.1,$$

$$d_1 = (b_1 + b_4)/2,\ d_2 = (b_2 - b_1)/2,$$

$$d_3 = (b_3 - b_2)/2,$$

$$d_4 = (b_4 - b_3)/2, \text{ and}$$

$$e = a + ((b_1 + b_4)/2)c_1 - ((b_2 - b_1)/2)c_1 - ((b_3 - b_2)/2)c_2 - ((b_4 - b_3)/2)c_3.$$

Our estimates of the above parameters and their standard errors are in Appendix Table 1.

Appendix table 1

Parameter estimates for segmented SL vs. OR regression model, and their associated standard errors (SE).

Parameter	Estimate	SE
e	12.375	0.411
d_1	0.0780	0.0078
d_2	−0.0507	0.016
d_3	0.0190	0.014
d_4	−0.0136	0.00091
c_1	3.872	0.480
c_2	7.310	2.044
c_3	43.131	2.128

Abstract.—A new species of ghost shrimp *Lepidophthalmus sinuensis* is described from the Caribbean coast of Colombia, and general ecological observations are made on the conditions under which it was found. The new species can be distinguished from others in the genus by the presence of large subrectangular lateral projections on the frontal region of the carapace. The new species was discovered in ponds of a commercial penaeid shrimp farm where its burrow densities range up to 2093 burrow openings/m^2 in pond bottoms consisting of fine sand. It appears that, on at least a temporary basis, activities of *L. sinuensis* may negatively impact penaeid shrimp culture.

Lepidophthalmus sinuensis: A New Species of Ghost Shrimp (Decapoda: Thalassinidea: Callianassidae) of Importance to the Commercial Culture of Penaeid Shrimps on the Caribbean Coast of Colombia, with Observations on its Ecology

Rafael Lemaitre

Smithsonian Oceanographic Sorting Center
National Museum of Natural History, Washington, DC 20560

Sérgio de Almeida Rodrigues

Departamento de Ecologia Geral, Instituto de Biociencias
Universidade de São Paulo, C. Postal 11461, 05499 São Paulo, SP, Brazil

During the first few months of 1990, penaeid shrimp production in several of the older ponds of a penaeid shrimp farm owned by the company Agrosoledad S.A. (located south of Cartagena, on the Caribbean coast of Colombia) began unexpectedly to decrease. Symptoms in the affected ponds during the grow-out cycles were: sustained low dissolved oxygen concentrations, an unusually high number of thalassinid burrows on the bottom, and small (unmarketable) shrimp in the harvest. About 50% of the ponds of the farm appeared to be affected. Other shrimp farms along this coast, however, were not affected. In July of 1990, biologists from the company, suspecting that the thalassinid might be the cause of the problem, sent specimens to one of us (RL) for identification. Our examination of the material revealed that the specimens represented a new species of the family Callianassidae. Subsequently, we traveled to the shrimp farm to obtain additional samples and make observations. Included herein is the description of this new species as well as some general ecological observations on the conditions under which it was found.

The discovery of this new callianassid is of significance to the rapidly growing industry of penaeid shrimp culture in Colombia. In 1990, the 1504 ha of ponds that were in production on the Caribbean coast alone produced a total harvest of 4314 metric tons of whole shrimp, valued at US$22.4 million. The shrimp produced is a mixture of *Penaeus vannamei* Boone, and *P. stylirostris* Stimpson. Although in Asian countries and western North America, thalassinids are known to cause damage to aquaculture operations, paddy fields, and engineering projects (e.g., Scharff and Tweedie 1942, Sankolli 1963, MacGinitie and MacGinitie 1968, ASEAN 1978), this is the first known case in the New World where a thalassinid has been proposed as potentially affecting penaeid shrimp mariculture.

The material of the new species has been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), Museu de Zoología da Universidade de São Paulo, Brazil

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Fishery Bulletin, U.S. 89:623–630 (1991).

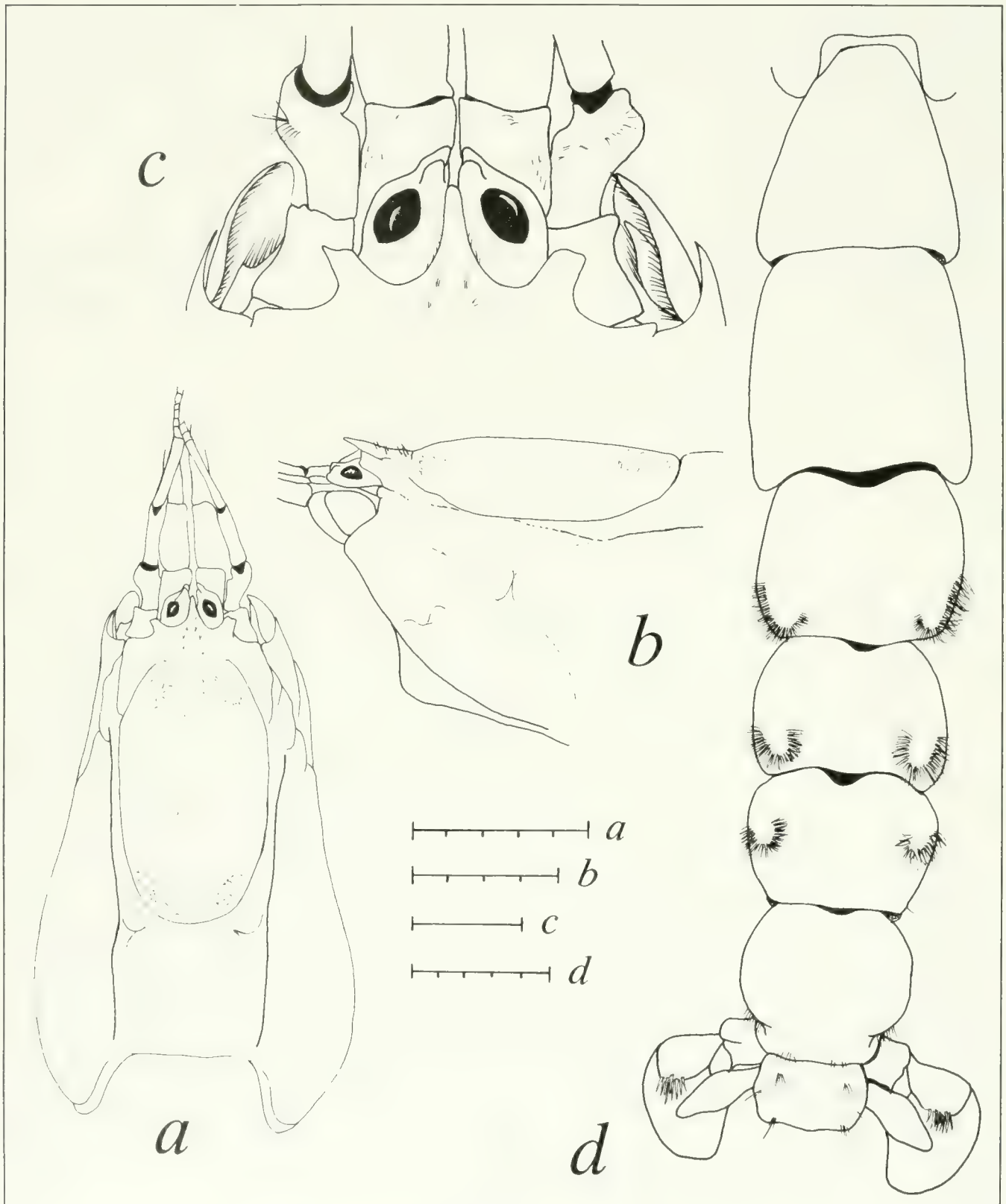

Figure 1

Lepidophthalmus sinuensis new species. (a) Carapace and cephalic appendages (dorsal view); (b) anterior portion of carapace and cephalic appendages (lateral view); (c) frontal region and cephalic appendages (dorsal view); (d) abdomen and tail fan (dorsal view). (a–c) Male CL 11.5 mm; (d) female CL 9.8 mm. Scales equal 5 mm (a, d), 4 mm (b), 1 mm (c).

(MZUSP), and in the zoological collections of the University of Southwestern Louisiana, Lafayette (USLZ). The abbreviation "CL" refers to carapace length measured along the dorsal midline from the level of the posterior orbital margin to the posterior end of the carapace. Two *in situ* burrow casts were made using epoxy resin (Araldit with hardener), following the method described by Dworschak (1983).

Lepidophthalmus sinuensis new species Figures 1–4

Material examined

Agrosoledad S.A. shrimp farm, 3 mi inland from mouth of Rio Sinú, Departamento de Cordoba, Colombia (9°17′N, 75°50′W): 1 ♂, holotype (CL 11.8mm), pond 5, 20 Aug. 1990, USNM 252399; 25 ♂ (CL 5.2–13.4 mm), 24 ♀ (CL 3.5–9.1mm), pond 5, 20 Aug. 1990, USNM 252400, 252401, MZUSP 10751, USLZ 3027; 5 ♂ (CL 4.9–11.6mm), 5 ♀ (1 ovig.) (CL 7.2–10.3mm), pond 7, 20 Aug. 1990, USNM 252402. Bungalow beach near San Bernardo del Viento, Departamento de Córdoba, Colombia (9°17′N, 76°00′W): 1 ♂ (CL 11.0 mm), 5 ♀ (1 ovig.) (CL 8.3–11.8mm), July 1990, coll. J. Araújo, USNM 252404, 252405; 3 ♂ (CL 10.5–13.8 mm), 7 ♀ (1 ovig.) (CL 8.6–13.2mm), drainage canal, 20 Aug. 1990, USNM 252403.

Description

Frontal margin of carapace with blunt rostral spine and two fixed subrectangular lateral projections (Fig. 1c); rostral spine and lateral projections directed slightly upward; rostral spine reaching to about 2/3 length of eyestalks, lateral projections reaching to about midlength of rostrum. Anterior margin of carapace level between subrectangular lateral projections and margin of antennal peduncle, then curving forward to anterolateral angle of branchiostegite. Dorsal oval about 0.6 times length of carapace, smooth, weakly delimited anteriorly.

Eyestalks reaching to about 2/3 length of basal antennular segment, terminating distally in two subtriangular blunt protuberances (shorter dorsal, larger ventral). Cornea small, pigmented, centrally situated on the eyestalk. Antennular peduncle stouter than antennal peduncle, first (basal) segment shorter than second; third segment about 2.5 times as long as second; second and third segments with dense setation on ventral margin; flagellum with subequal rami. Antennal peduncle reaching to about midlength of ultimate antennular segment; flagellum about twice as long as antennular flagellum.

Mandible with several teeth on molar process, and long two-segmented palp. Maxillule with endopod curved distally. Maxilla, first and second maxillipeds as figured (Fig. 2c–e). Third maxilliped with slender, curved dactyl shorter and narrower than propodus; propodus about as long as wide, outer surface naked, inner surface with tuft of setae on posterior half; carpus with tuft of setae on inner surface near distal margin; with rudimentary exopod.

Branchial formula:

	maxillipeds			pereopods				
	1	2	3	1	2	3	4	5
Pleurobranchs	—	—	—	—	—	—	—	—
Arthrobranchs	—	1*	2	2	2	2	2	—
Podobranchs	—	—	—	—	—	—	—	—
Epipods	1	1	—	—	—	—	—	—
Exopods	1	1	1*	—	—	—	—	—

* rudimentary

Chelipeds strongly dissimilar, major cheliped on right or left side. Sexual dimorphism evident on major and minor chelipeds. Major cheliped of male (Fig. 3a) massive, reaching to about tip of antennal flagellum. Fingers leaving large gap proximally when closed. Dactyl longer than palm, smooth except for tufts of setae on dorsal margin and on basal outer surface of teeth; prehensile edge with 4–6 large, unequal, rounded teeth; inner face of dactyl with deep longitudinal groove. Fixed finger with strong tooth (pointing slightly outward and forward) near middle of prehensile edge and under second tooth of dactyl. Palm with scattered tufts of setae on outer face, row of tufts of setae on dorsal margin, and tufts of very long setae (reaching to about 2/3 length of dactyl) near dorsomesial distal angle; dorsal and ventral margin defined by keel-like ridge; outer face with several small tubercles bearing tufts of setae on sloping depression near base of fixed finger; inner face of palm (Fig. 3b) with tubercles bearing tufts of setae on ventromesial margin and on sloping depression near base of fixed finger. Carpus longer than palm, broader than long, dorsal and ventral margin defined by keel-like ridge, with small blunt tooth on dorsodistal and ventrodistal angle. Merus about as long as carpus, with row of three blunt spines on ventromesial distal margin. Ischium slender, slightly shorter than merus, armed with row of 14 small spines on ventrolateral margin.

Major cheliped of female strong but shorter, less high than in male. Fingers with tips strongly curved inward, crossing when closed; prehensile edge of dactyl and fixed finger straight or irregular (Fig. 3d, e), with small rounded teeth; fixed finger usually with strong, sharp tooth basally on outer face. Merus with ventromesial distal row of blunt to sharp spines, and usually with

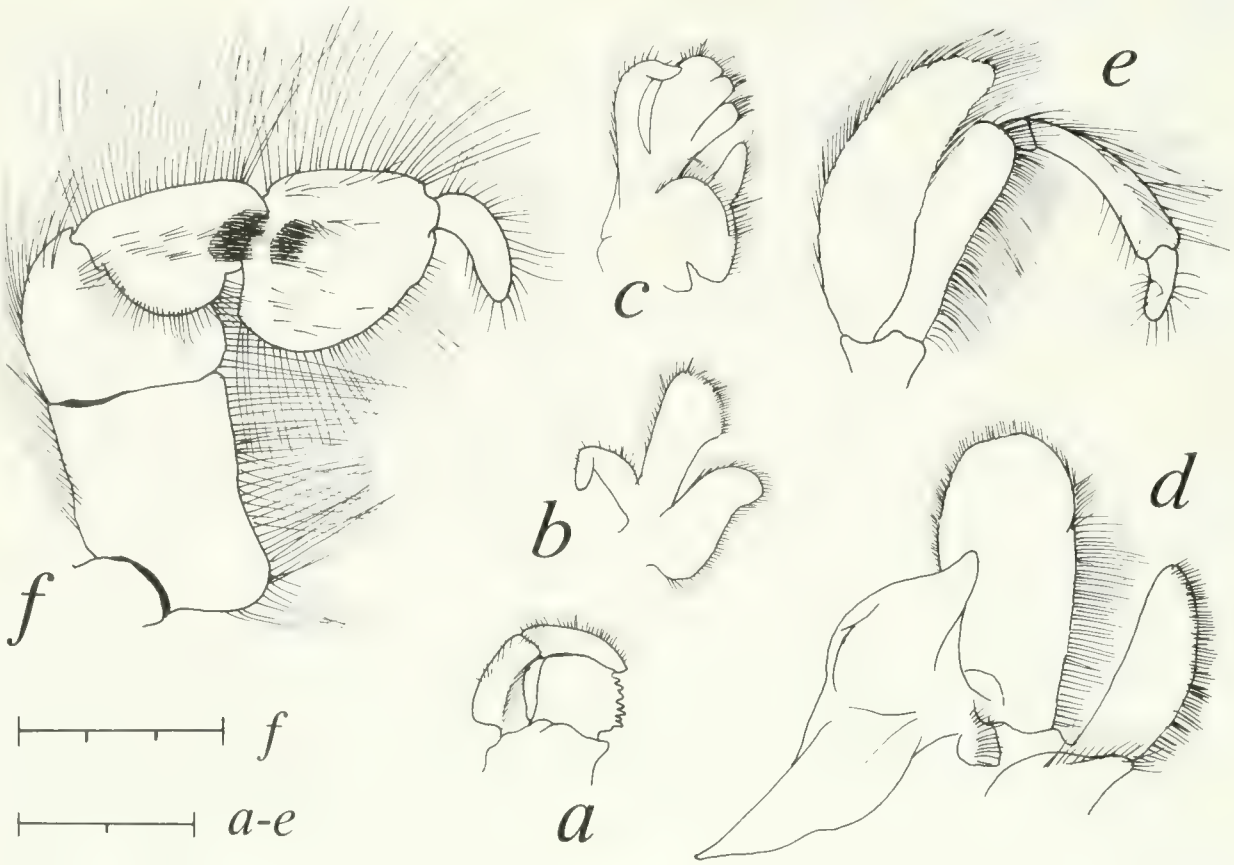

Figure 2

Lepidophthalmus sinuensis new species. Mouthparts (internal view): (a) mandible; (b) maxillule; (c) maxilla; (d) first maxilliped; (e) second maxilliped; (f) third maxilliped (exopod not shown). Male CL 11.5mm. Scales equal 2mm (a–e) and 3mm (f).

slender, curved spine on lateroproximal angle. Ischium with row of 16–17 small spines on ventrolateral margin.

Minor cheliped of male reaching to about level of bases of fingers of major cheliped. Fingers gaping when closed; prehensile edges of fingers formed by ridge of small rounded teeth. Dactyl with row of tufts of setae on dorsal and ventrolateral margin. Fixed finger with dense, brush-like setae basally on prehensile edge (Fig. 3c). Merus with slender curved spine on lateroproximal angle. Ischium with row of 18 small spines on ventrolateral margin.

Minor cheliped of female similar to that of male but somewhat slenderer, lacking brush-like setae on fixed finger.

Second pair of pereopods chelate, subequal; margins of chela and carpus setose; ventral margin of merus with row of evenly spaced long setae. Third pereopod with dactyl slightly longer than broad, subtriangular. Margins of dactyl and propodus with long setae. Propodus with ventral margin divided into three unequal lobes (medial one smallest); outer face covered with numerous tufts of short setae. Fourth pereopod subchelate; propodus and dactyl with setae, densely setose grooming apparatus on ventral margin of propodus. Fifth pereopod subchelate; propodus and dactyl with setae, densely setose grooming apparatus on suboval area covering most of inner face of propodus.

Abdominal somites smooth; dorsal surface naked except for line of dense setae forming sub-semioval near posterolateral angles of each somites 3 and 4 and on midline of somite 5, and line of short setae on posterolateral angle of somite 6 (Fig. 1d). Male first pleopod uniramous, two-segmented (Fig. 4c); distal segment with long setae, terminating in subtriangular tip with small lobe at base on anterior margin; basal segment two times (or more) as long as distal segment. Male second pleopod biramous, with appendix interna on endopod (Fig. 4d). Female first pleopod uniramous,

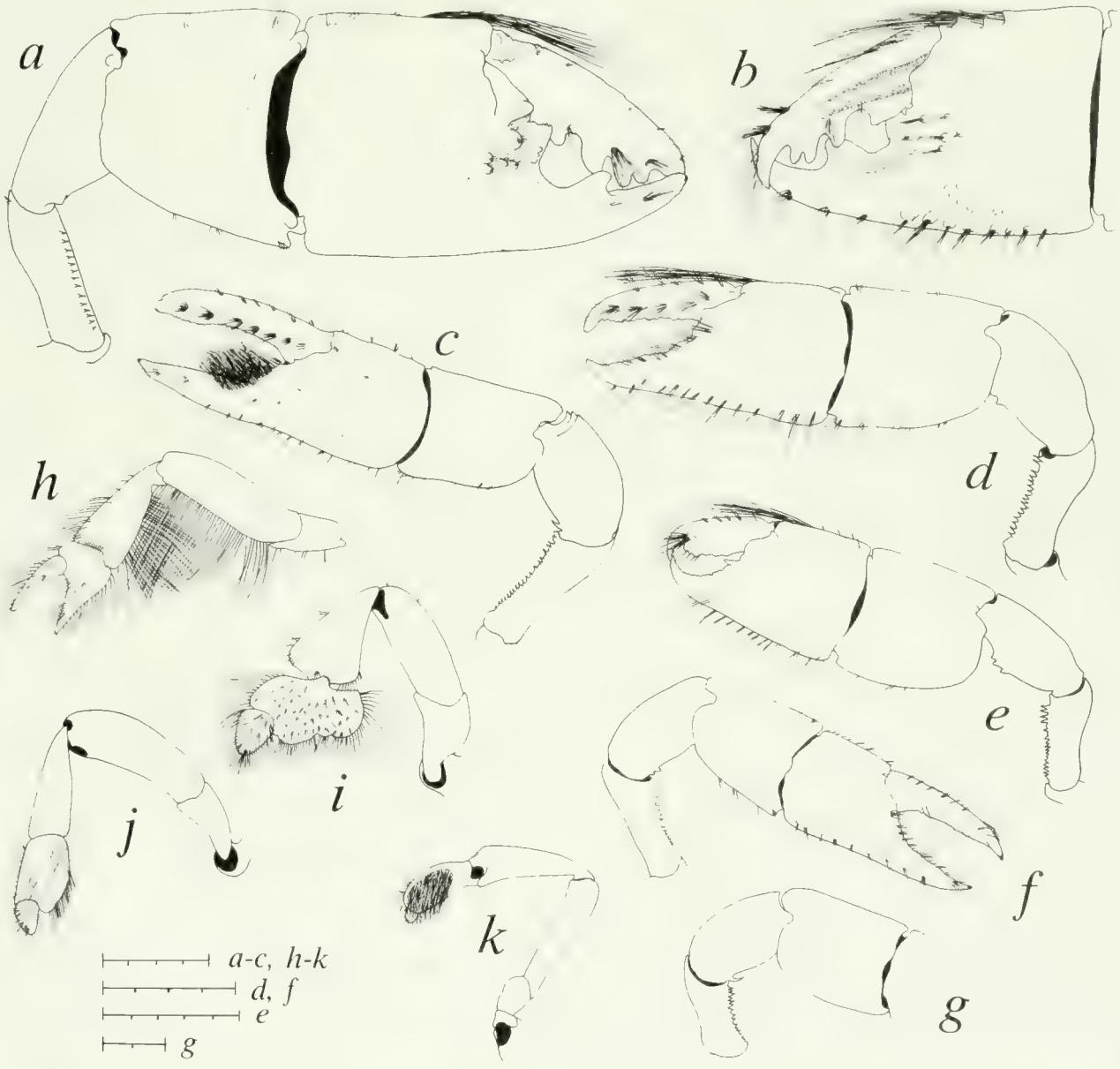

Figure 3

Lepidophthalmus sinuensis new species. (a) Male major cheliped (lateral view); (b) male chela (internal view); (c) male minor cheliped (lateral view); (d, e) female major cheliped (lateral view); (f) female minor cheliped (lateral view); (g) ischium, merus, and carpus of female minor cheliped (lateral view); (h–k) left pereopods: (h) second, (i) third, (j) fourth, (k) fifth. (a–c, h–j) Male CL 11.5 mm; (d, f) female 9.8 mm; (e, g) female CL 9.0 mm; (k) male 10.0 mm. Scales equal 4 mm (a–d, f, h–k), 5 mm (e), and 2 mm (g).

two-segmented (Fig. 4e); distal segment setose, with sinuous anterior margin; basal segment bent in midline at about right angle. Female second pleopod biramous (Fig. 4f), with appendix interna on endopod. Third to fifth pleopods large, strong (Fig. 4g); each pair forming a subcircular fan when linked together by appendix interna; exopod leaf-like, endopod subtriangular.

Telson subrectangular, about 1.4 times as wide as long (Fig. 4b); dorsal surface smooth, with two pairs of tufts of setae (one on anterior half, one near posterolateral angle); lateral margins convex; posterior margin weakly divided into large, medial, broadly rounded lobe, and two rounded lateral lobes. Uropod with protopodite-bearing spine on posterolateral angle;

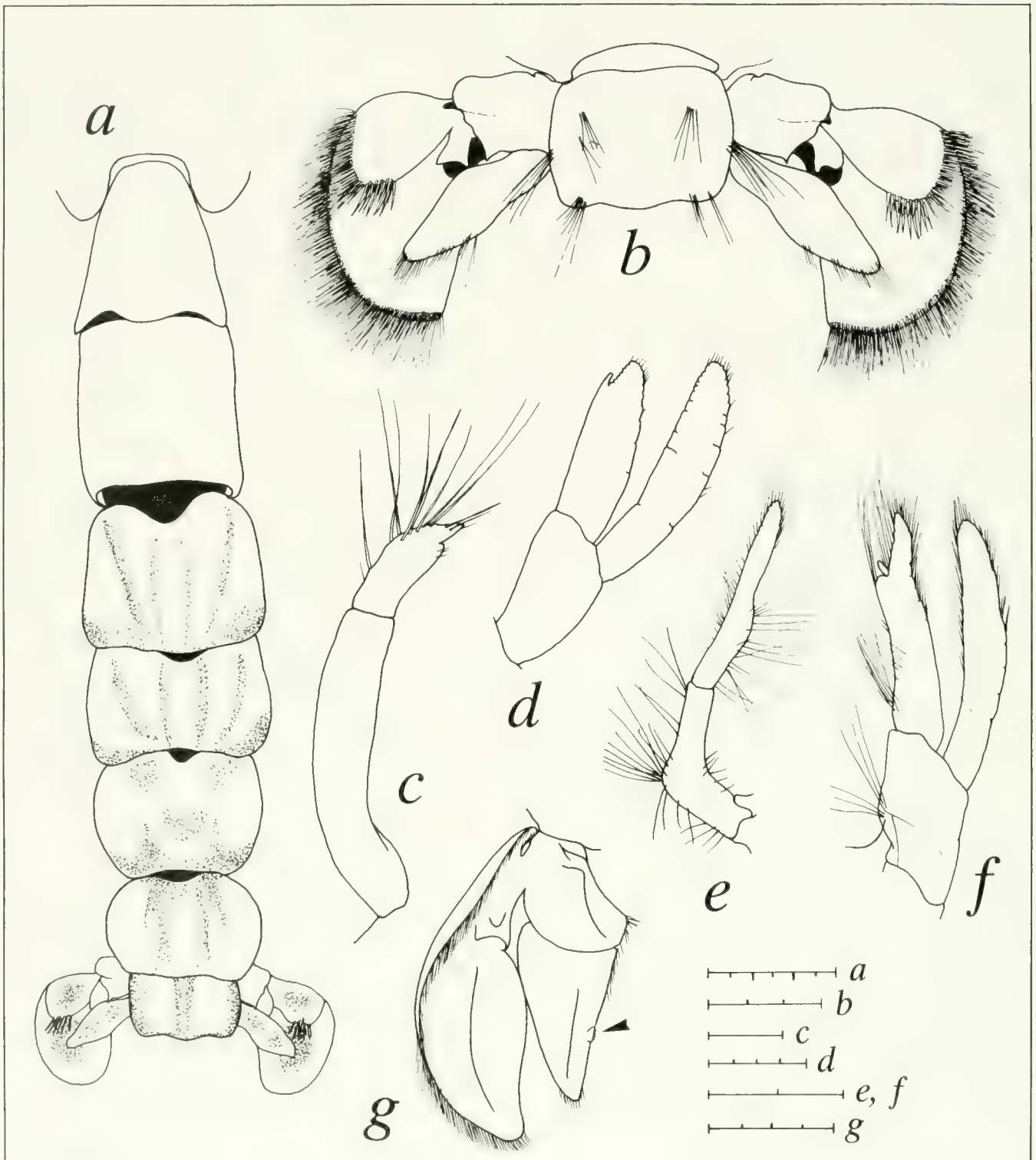

Figure 4

Lepidophthalmus sinuensis new species. (a) Abdomen and tailfan (dorsal view; setae omitted), showing color pattern (stippled areas); (b) telson and uropods (dorsal view); (c) male left first pleopod (lateral view); (d) male left second pleopod (posterior view); (e) female left first pleopod (lateral view); (f) female left second pleopod (lateral view); (g) third left pleopod (posterior view; arrow indicates appendix interna). (a) Female CL 11.3 mm; (b–d, g) male CL 11.5 mm; (e, f) female 9.8 mm. Scales equal 6 mm (a), 3 mm (b), 0.5 mm (c), 4 mm (d, g), and 2 mm (e, f).

endopod narrow, more than 2.5 times as long as broad, distal half slightly bent ventrally; upper exopodal plate shorter and smaller than lower exopodal plate, with rows of long, slender corneous spines on posterolateral margin; lateral margin of exopodal plates with dense setation.

Coloration (Fig. 4a)

In life, carapace transparent except for white frontal region. Chelipeds and pereopods 2–5 white, with densely setose areas brownish or dark orange. Abdomen with somites 1, 2 transparent; dorsal surface of somites 3–6 with olive patterns as follows: somite 3, 4 with stripes on each side of midline, and one stripe on each side forming a "V"; somite 5 with 3 patches on anterior 2/3 (each patch located on ends of inverted triangle), and band on posterior margin forming a triangle on each side of midline; somite 6 with two stripes on each side of midline. Telson with three olive stripes (one medial, one on each side adjacent to lateral margin). Uropod olive, with darker areas on central part of exopodal plates and endopod.

Distribution

Caribbean coast of Colombia: so far known only from Agrosoledad S.A. shrimp farm, near the mouth of the Sinú River, on the southern coast of the Golfo de Morrosquillo, and south of the farm at a beach near the town of San Bernardo del Viento. Intertidal, and in shrimp ponds at about 1.5 m depth.

Etymology

The specific name is given in honor of the Sinú indians, original inhabitants of the area where the new species was found.

Remarks

The traditional division of the family Callianassidae (Borradaile 1903, de Man 1928a, b) has been under constant criticism by recent authors (de Saint Laurent 1973 and 1979, Manning and Felder 1986, Manning 1987, Sakai 1987). For example, some of the American species that in the past were in the genus *Callianassa* Leach, 1814, are now being reassigned to other genera previously considered junior synonyms of *Callianassa*. This new species is placed in *Lepidophthalmus* Holmes, 1904, a genus recently resurrected by Manning and Felder (In press).

Lepidophthalmus sinuensis can be easily distinguished from the other species in the genus—*L. bocourti* (Milne Edwards 1870) from the eastern Pacific, and *L. louisianensis* (Schmitt 1935) and *L. jamaicense* (Schmitt 1935) from the western Atlantic—by the presence in the new species of large subrectangular projections of the frontal region of the carapace. Other differentiating characters observed in *L. sinuensis* are: the sexual dimorphism shown in the minor cheliped with brush-like setae on the fixed finger of males (lacking in females); the distal segment of the male first pleopod that is weakly divided distally; and the endopod of the uropod that is very slender and bent distally.

Ecological observations

Specimens of *Lepidophthalmus sinuensis* were obtained in penaeid shrimp ponds of about 10 ha each, and in a natural habitat on a beach site west of the shrimp farm. Individuals were easily collected by digging with a shovel or using a yabby pump, a suction device of the type described by Reaka and Manning (1989). Salinities in the ponds ranged from 15 to 25‰. The type of sediment where the new species was found is a very fine grey sand. In one pond with both fine sand and clayish bottom sections, *L. sinuensis* was absent in the clayish section whereas it was abundant in the fine-sand section. Therefore, *L. sinuensis* does not appear to survive in clayish sediment.

The number of burrow openings in the ponds most heavily populated with this callianassid ranged from 1894 to 2093 burrow openings/m^2. Resin casts of the burrows indicate that many have double openings and are Y-shaped. A conservative estimate of the population density in these ponds probably is about half the burrow density (947–1046 individuals/m^2). These densities are among the highest recorded for adult thalassinids. Dworschak (1987) has reported a density of 2420 burrow openings/m^2 of juvenile *Upogebia pusilla* (Petagna), quoting this number as the highest ever reported, and Griffis (1990) found a maximum density of slightly less than 1400/m^2 of juveniles of *Callianassa gigas* Dana.

The great proliferation of *Lepidophthalmus sinuensis* in penaeid shrimp ponds can be attributed, possibly, to one or a combination of the following factors: (1) abundant supply of food due to the high productivity that is artificially produced during the penaeid grow-out cycle (e.g., by addition of fertilizers such as chicken manure, urea, and pelleted food); (2) availability of a large area of undisturbed, stable sand, ideal for the construction of burrows; (3) concentration and increased survival of callianassid larvae in an enclosed area at the time of transition from the planktonic to the benthic stage; and (4) the ability to survive the drying stages of the ponds between grow-out cycles (one pond left dry for 45 days still had a population of live *L. sinuensis*). Callianassids are known to influence sediment

characteristics, benthic communities, and the release of nutrients into the water column (Ott et al. 1976, Posey 1986a,b). The nature of their effect on the penaeid culture is unknown. Based on our observations it appears that, at least during some growing cycles, the activity of *L. sinuensis* can prevent pond-grown penaeid shrimp from reaching a marketable size and weight. However, the exact short-term and long-term effects caused by this new species on the culture will have to be investigated.

Acknowledgments

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Abstract.—The diel pattern in vertical distribution of red drum *Sciaenops ocellatus* larvae was described from plankton collections taken at three depths and three time periods over a 24-hour period during five cruises in inner shelf waters of the northcentral Gulf of Mexico (east Louisiana–Mississippi–Alabama region). Larvae ranging in mean size from 1.7 to 5.0 mm were vertically stratified at both offshore and nearshore locations over bottom depths <25 m. Diel periodicity in vertical stratification was evident in four cruises, with larvae being concentrated higher in the water column during daylight hours than at night. There was no clear relationship between vertical aggregation of red drum larvae and temperature or salinity profiles or prey microzooplankton distribution.

Diel Vertical Distribution of Red Drum *Sciaenops ocellatus* Larvae in the Northcentral Gulf of Mexico

Joanne Lyczkowski-Shultz
John P. Steen Jr.

Gulf Coast Research Laboratory
P.O. Box 7000, Ocean Springs, Mississippi 39564

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Diel vertical migration has been observed among the larvae of many taxa of marine fishes in diverse environments ranging from estuaries to the open sea (see Neilson and Perry 1990 for recent review), and under both stratified and well-mixed hydrographic conditions (Ahlstrom 1959, Smith et al. 1978, Kendall and Naplin 1981, Brewer and Kleppel 1986, Perry and Neilson 1988). The most frequently observed pattern of larval movement has been daytime concentration at lower depths with subsequent movement towards the surface at night (Smith et al. 1978, Kendall and Naplin 1981, Boehlert et al. 1985), but the reverse tendency has also been noted (Hempel and Weikert 1972, Boehlert et al. 1985, Yamashita et al. 1985, Sogard et al. 1987, Neilson and Perry 1990). Another pattern is one where larvae are aggregated at depth during daytime but become more dispersed at night (Brewer and Kleppel 1986, Heath et al. 1988). Ontogenetic differences in vertical distribution and migration patterns have frequently been observed (Brewer and Kleppel 1986, Castonguay and McCleave 1987, Stephenson and Power 1988). The adaptive significance of vertical migration remains unknown (Pearre 1979), but some inferred or proposed advantages to fish larvae include maintenance of position relative to prey (Hunter and Sanchez 1976); predator avoidance (Zaret and Suffern 1976); energy conservation through swimbladder inflation at the surface (Hunter and Sanchez 1976); maximization of energy intake through depth-mediated thermoregulation (Wurtsbaugh and Neverman 1988); and enhancement of transport to nursery grounds (Miller et al. 1984, Norcross and Shaw 1984, Boehlert and Mundy 1988). Knowledge of vertical distribution patterns among early life stages is necessary, not only to better understand early ecology but also to improve the design of broadscale surveys for resource and population assessments using the abundance of fish eggs and larvae (Ahlstrom 1959, Stephenson and Power 1988, Perry and Neilson 1988).

Data presented here on diel changes in vertical distribution of red drum *Sciaenops ocellatus* larvae came from an ongoing, comprehensive investigation begun in 1983 into the early ecology (Lyczkowski-Shultz et al. 1988), age and growth (Comyns et al. 1989), and spawning seasonality and biomass (Comyns et al. 1991) of this commercially and recreationally valuable sciaenid in coastal and shelf waters of the northern Gulf of Mexico.

Materials and methods

Ichthyoplankton collections were taken during five, 24-hour cruises in September and October 1984 and 1985 in the general area east of the Mississippi River delta and south of the Mississippi barrier islands over the east Louisiana–Mississippi–Alabama shelf (Fig. 1). Discrete-depth

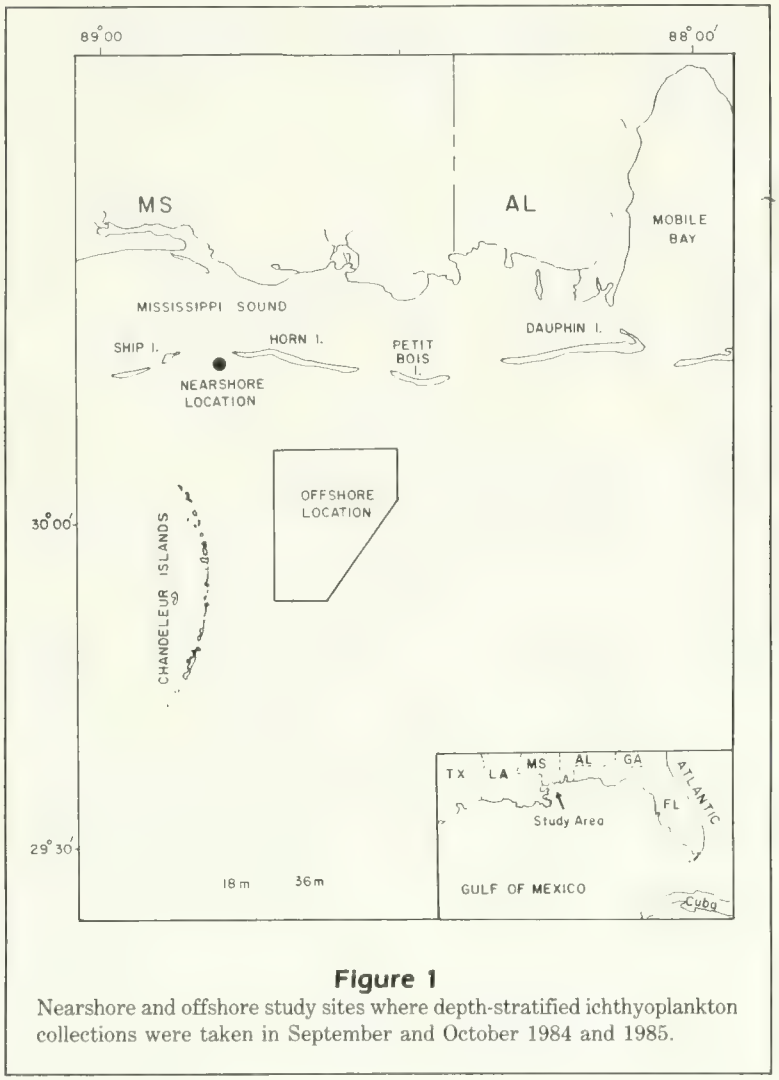

Figure 1
Nearshore and offshore study sites where depth-stratified ichthyoplankton collections were taken in September and October 1984 and 1985.

samples were taken offshore in the vicinity of a "windowshade," subsurface (5m) current drogue as it was tracked from the ship throughout the duration of a cruise in an attempt to repeatedly sample the same patch of fish larvae and zooplankton (Lyczkowski-Shultz et al. 1988). The drogue traveled, on average, 13km during a sampling period, typically at varying compass headings over water depths of 18–25m. During each cruise, collections were usually made during early to late afternoon of the first day, then in the middle of the night (usually prior to midnight), and in the morning (after sunrise) of the second day. In all but one instance, dawn and dusk periods were specifically avoided. Times of sunrise and sunset on sampling dates in September and October 1984 and 1985 ranged from 0543 to 0600 hours, and from 1733 to 1819 hours central standard time (CST), respectively. During three of the five cruises, additional samples were taken at a fixed, shallow water station (12m) located 15–19km NNW of the offshore sampling area during midday hours of the second day (nearshore, Fig. 1). Times of high and low tide were determined using predictions for tide stations nearest the offshore sampling sites (NOAA-NOS Tide Tables).

Sampling gear consisted of a 1×1.4m, multiple-net Tucker trawl with an effective mouth opening of $1 m^2$ when fished at a 45° angle, and a double-release mechanism operated manually with messengers. Mean tow speeds varied from 1.5 to 2.5 knots (0.8–1.3m/s). At the offshore location, three Tucker trawl casts were made during each time period. A cast consisted of all three 333-μ mesh nets being fished in horizontal 5-min hauls at one nominal depth level at a time. These sampling depths were 1, 5, and, most typically, 11 or 12m. At the nearshore location, each of the three nets were fished at 1, 3, and 7 or 9m, but the nets were of different mesh sizes: 333, 505, and 760μ. Offshore catch data from the three net samples at each depth were pooled for analyses for cruises 84-9-1, 84-10-1, and 85-9-1, even though only net 2 was both opened and closed at depth. Contamination in nets 1 and 3 was considered to be minimal due to the relatively short time for their deployment and retrieval, less than 30 seconds in total. Comparison of catches from the three nets indicated that contamination had not seriously affected our results, as there was little to no overlap among adjacent sampling depths in the range of observed densities (as measured by each of the three nets) per sampling period (Fig. 2). Catch data from all three nets of different mesh sizes at the nearshore site were combined since sampling effort, i.e., number of samples per mesh size at each depth, was the same. Due to time constraints, only net 2 samples (the 333-μ mesh net at the nearshore site) were sorted from cruises 84-9-2 and 85-10.

Fishing depth was monitored throughout each tow via the depth sensor of an electronic conductivity/temperature/depth probe package (CTD) which was mounted 0.5m above the trawl frame on the conducting/towing cable. Except for the nearsurface or 1m depth stratum, actual sampling depths exceeded nominal depths by 0.5m. Target or nominal sampling depths were maintained throughout each tow by adjusting the amount of wire out.

Flowmeters in each net measured volume filtered which generally ranged between 200 and 300 m^3.

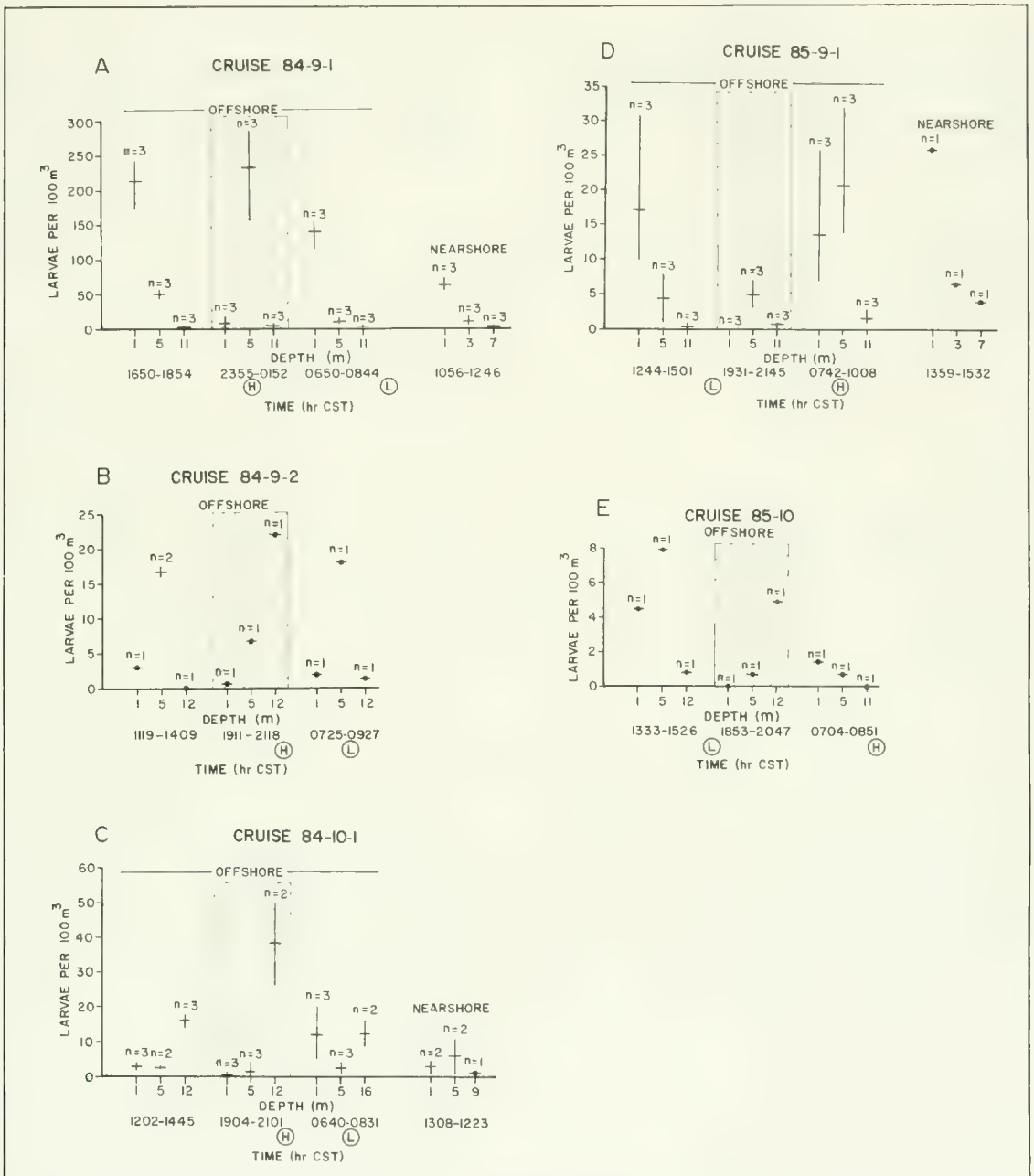

Figure 2

Mean and range in density of red drum larvae *Sciaenops ocellatus* by sampling depth and time at offshore and nearshore sites during cruises in 1984 and 1985. n = number of collections per sampling period. Crosshatching denotes nighttime observations. Encircled H and L symbols mark the approximate times of high and low tide.

Vertical profiles of temperature and salinity prior to sample collection were obtained with the CTD.

Ichthyoplankton samples were preserved at sea in 5–10% formalin and were later (1 week to 6 months) transferred to 70% ethanol for final preservation. In the laboratory, all larvae were removed from either the entire sample or from a one-half aliquot which was obtained using a Motoda plankton splitter (Van Guelpen et al. 1982). Standard length (SL) of larvae was measured to the nearest 0.1 mm at 12× using a stereomicroscope. Larval densities are reported as number per 100 m^3.

Zooplankton samples were collected by pumping water up from the same depths as ichthyoplankton

collections with a 38 L/min capacity diaphram pump and filtering approximately 0.3–0.5 m^3 through nested 63 and 25 μ mesh nets on deck. Zooplankton samples were preserved in 5% formalin. The average time between collection of fish larvae and zooplankton was 2.5 hours, with values ranging between 21 minutes and 4 hours.

Statistical analysis of diel vertical patterns in larval red drum abundance was conducted using nonstandard, chi-squared, goodness-of-fit procedures (McCleave et al. 1987). First, the standardized residual of larval density at each depth was calculated,

$$SR_i = \frac{(N_i - E_i)}{\sqrt{E_i}}$$

where N_i = observed catch at depth i, and E_i = expected catch at depth i. E_i was calculated by multiplying the total number of red drum larvae caught during a time period (all depths combined) by the proportion of total fishing effort at that depth, i.e., the volume filtered at that depth divided by the total volume filtered during the time period. The sum of squared SR_i's yields the chi-squared (χ^2) statistic for testing the null hypothesis that within a single time period the density of red drum larvae is uniform with depth. A second null hypothesis—that the vertical distribution of larvae remains unchanged over the diel cycle, i.e., among the three sampling periods—was investigated using the chi-squared test for heterogeneity (a nonstandard, goodness-of-fit test; Sokal and Rohlf 1981). This was accomplished by subtracting the χ^2 value for the combined data set (three time periods) from the sum of the individual χ^2's for each time period.

Results

Depth-stratified ichthyoplankton collections during afternoon, night, and morning, over a 24-hour period during five cruises, were examined for patterns in vertical distribution of red drum larvae. Larvae were vertically stratified in both offshore and nearshore waters (Fig. 2). Larvae were usually more abundant at 1 and/or 5 m than at 11, 12, or 16 m at the offshore location, and than at 7 or 9 m at the nearshore location. In two of the three cruises in which both offshore and nearshore sites were sampled, the depth of greatest abundance (at a comparable time period) was the same at both nearshore and offshore sites (Fig. 2A, D).

Vertical stratification at the offshore location appeared to have a diel component in four cruises (Fig. 2A, B, D, E). The most consistent diel pattern was a decrease in abundance, relative to afternoon values, at 1 m and a relative increase at 5 or 11–12 m during nighttime hours. The following morning, abundance at 1 and/or 5 m was higher than the nighttime values at those depths. During cruise 84-9-2 the diel shift in maximum abundance occurred between 5 and 12 m, with abundance at 1 m remaining relatively constant throughout the 24-hour period (Fig. 2B). Mean density of larvae during cruise 84-10-1 was highest at 12 m during both afternoon and night, but in the morning maximum density values were observed at both 1 and 16 m (Fig. 2C).

The most distinct pattern of vertical stratification was observed in cruise 84-9-1 where the center of abundance of red drum larvae shifted from 1 to 5 m and back to 1 m over the three time periods, with no overlap in mean density or range in densities among adjacent depths within a sampling period (Fig. 2A). Mean density at 1 m in the afternoon was remarkably similar to the mean density at 5 m at night, 214.5 vs. 234.5, but by morning of the next day maximum abundance had declined to 141.0. Although vertical stratification was evident in the other three offshore data sets, the diel pattern was less distinct.

Nonstandard, chi-squared goodness-of-fit analyses were used to test two null hypotheses (McCleave et al. 1987): that (1) red drum larvae were homogeneously distributed over the three sampling depths, and (2) the vertical distribution of larvae remained unchanged over three sampling times spanning a diel cycle. In 17 of 18 cases, including both offshore and nearshore sites, null hypothesis 1 was rejected at the 0.01 significance level (Tables 1 and 2). In all five data sets from the offshore site, null hypothesis 2 was also rejected at the 0.01 significance level, i.e., larval depth distribution did not remain the same among the sampling periods (Table 1).

The sign and magnitude of standardized residual deviations, SR_i values, were examined to determine the diel pattern in vertical distribution of red drum larvae (Table 1). In four of five cruises, the depth of greatest larval abundance was higher in the water column during afternoon hours than at night (Fig. 2). In two cruises (84-9-1 and 84-9-2), the depth of greatest larval abundance on the following morning was the same as on the preceding afternoon and, therefore, higher in the water column than on the preceding night. In one cruise (85-9-1), although the depth of greatest abundance (5 m) in the morning was the same as at night, abundance at 1 m (depth of greatest abundance during the preceding afternoon) had increased relative to the nighttime value. The morning sampling period of cruise 85-10 was the only case where larvae were homogeneously distributed throughout the water column. During the only cruise (84-10-1) in which depth of greatest larval abundance was the same in afternoon

Table 1

Analyses of the null hypotheses: (1) red drum larvae are homogeneously distributed over three sampling depths, and (2) the vertical distribution of larvae is similar over three sampling times spanning a diel cycle. Data from five cruises from offshore Mississippi waters in September and October, 1984 and 1985. N_i = number of larvae at depth i; E_i = expected number of larvae at depth i; SR_i = standardized residual deviation of observed from expected catch at depth i.

	Afternoon (1650–1854 hrs)				Night (2355–0152 hrs)				Morning (0650–0844 hrs)				Times combined		
Depth	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	N_i	E_i	SR_i
Cruise 84-9-1, 13–14 September 1984															
1	835	1807	757	+38	647	63	587	−22	722	993	336	+36	2863	1680	+29
5	610	308	553	−0	916	2217	830	+48	741	84	345	−14	2609	1728	+21
11	896	8	812	−28	1011	53	917	−28	938	41	437	−19	102	2166	−44
Total	2341	2123			2575	2333			2401	1118					
Chi-square χ^2				2360**				3600**				1841**			3248

$\chi^2_{tot\ 2df} = 9.21$

$\chi^2_{het} = \chi^2_{aft} + \chi^2_{night} + \chi^2_{morn} - \chi^2_{comb} = 7801 - 3248 = 4553^{**}$

$\chi^2_{tot\ 4df} = 13.28$

	Afternoon (1119–1409 hrs)				Night (1911–2118 hrs)				Morning (0725–0927 hrs)				Times combined		
Depth	Volume	N	E_i	SR_i	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	N_i	E_i	SR_i
Cruise 84-9-2, 26–27 September 1984															
1	415	12	33	−0.4	382	2	36	−6	209	4	17	−3	18	85	−7
5	432	72	34	+6	387	26	36	−2	332	60	27	+6	158	97	+6
11	208	0	17	−4	346	76	32	+8	307	4	25	−4	80	73	+0.8
Total	1055	84			1114	104			847	68					
χ^2				58**				94**				69**			92

$\chi^2_{het} = 220 - 92 = 128^{**}$

	Afternoon (1202–1445 hrs)				Night (1904–2101 hrs)				Morning (0640–0831 hrs)				Times combined		
	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	N_i	E_i	SR_i
Cruise 84-10-1, 10–11 October 1984															
1	986	30	73	−5	741	2	113	−10	700	83	61	+3	115	221	−7
5	978	28	72	−5	752	10	115	−10	769	19	67	−6	57	228	−11
12(16)	998	160	73	+10	833	344	128	+19	982	112	86	+3	616	287	+19
Total	2962	218			2325	356			2451	214					
χ^2				154**				573**				50**			557

$\chi^2_{het} = 777 - 557 = 220^{**}$

	Afternoon (1244–1501 hrs)				Night (1931–2145 hrs)				Morning (0742–1008 hrs)				Times combined		
	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	N_i	E_i	SR_i
Cruise 85-9-1, 11–12 September 1985															
1	721	131	47	+12	666	0	13	−4	677	92	70	+3	223	130	+8
5	779	36	51	−2	652	34	13	+6	636	130	66	+8	200	130	+6
11	1103	2	72	−8	667	6	13	−2	984	16	102	−9	24	187	−12
Total	2603	169			1985	40			2297	238					
χ^2				223**				51**				142**			246

$\chi^2_{het} = 416 - 246 = 170^{**}$

	Afternoon (1333–1526 hrs)				Night (1853–2047 hrs)				Morning (0704–0851 hrs)				Times combined		
	Volume	N_i	E	SR	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	N	E_i	SR_i
Cruise 85-10, 10–11 October 1985															
1	224	10	10	+<0.1	305	0	6	−2	286	4	2	+1	14	18	−0.9
5	254	20	11	+3	285	2	5	−1	286	2	2	−<0.1	24	19	+1
12(11)	240	2	11	−3	284	14	5	+4	281	0	2	−1	16	18	−0.5
Total	718	32			874	16			853	6					
χ^2				14**				22**				4ns			3

$\chi^2_{het} = 400 - 3 = 37^{**}$

Table 2

Analyses of the null hypothesis: red drum larvae are homogeneously distributed over three sampling depths at the nearshore site. N_i = number of larvae at depth i; E_i = expected number of larvae at depth i; SR_i = standardized residual deviation of observed from expected catch at depth i.

Cruise 84-9-1					Cruise 84-10-1					Cruise 85-9-1				
Depth	Volume	N_i	E_i	SR_i	Depth	Volume	N_i	E_i	SR_i	Depth	Volume	N_i	E_i	SR_i
1	757	469	169	+23	1	706	20	35	3	1	591	84	53	+4
3	847	94	189	−7	5	1025	81	51	+4	3	275	18	25	−1
7	1025	25	229	−13	9	393	4	19	−4	7	498	20	45	−4
Total	2629	588				2124	105				1364	122		
χ^2				761**					37**					34**

$\chi^2_{.01,2df}$ = 9.21

Table 3

Mean standard length in millimeters (standard error of the mean in parenthesis) of red drum larvae at three sampling depths and time periods (afternoon, night, and morning) during five cruises in offshore waters.

Depth	Afternoon	Night	Morning
	Cruise 84-9-1		
1	2.8 (0.02)	2.7 (0.03)	2.9 (0.02)
5	2.7 (0.02)	2.7 (0.02)	2.6 (0.05)
11	2.8 (0.12)	2.7 (0.05)	2.6 (0.06)
	Cruise 84-9-2		
1	2.9 (0.13)	1.8 (—)	2.3 (0.48)
5	2.5 (0.04)	2.9 (0.04)	2.7 (0.08)
12	—	2.9 (0.05)	2.6 (0.68)
	Cruise 84-10-1		
1	4.7 (0.31)	3.8 (—)	4.4 (0.15)
5	4.0 (0.24)	4.6 (0.27)	4.3 (0.29)
12 (16)	3.9 (0.11)	4.5 (0.11)	4.0 (0.09)
	Cruise 85-9-1		
1	4.7 (0.05)	—	1.9 (0.13)
5	4.4 (0.11)	4.6 (0.20)	2.1 (0.14)
11	4.6 (—)	5.0 (0.31)	1.7 (0.02)
	Cruise 85-10		
1	3.7 (0.15)	—	3.3 (0.16)
5	3.4 (0.11)	4.6 (—)	4.4 (—)
12 (11)	1.3 (—)	3.6 (0.11)	—

and night sampling periods, there was an increase in abundance at 1 m in the morning hours with mean densities at 1 and 16 m being identical.

Size composition of red drum larvae within cruises remained relatively constant except during cruise 85-9-1 when mean size in the morning was much smaller than during two previous sampling periods (Table 3). Red drum larvae did not appear to be depth-stratified by size.

Vertical profiles of temperature and salinity taken just prior to sampling during each of the five cruises consistently showed the water column to be well-mixed (Fig. 3). There was no evidence of a well-defined or persistent thermocline to which red drum larvae might orient. Mean temperature averaged over sampling depths was 3°C higher during cruises 84-9-1&2 and 85-9-1 than during cruises 84-10-1 and 85-10. Salinity varied somewhat more throughout the water column than did temperature but usually differed no more than 2–3 ppt between September and October observations. Isohaline conditions generally prevailed within the upper 12 m of the water column during all cruises except 84-9-1, when a difference in salinity of 5 ppt between the surface and 12 m was observed throughout all three sampling periods (Fig. 3A). Yet the same general pattern in vertical stratification of red drum larvae was evident within that salinity gradient as was observed under more isohaline conditions. There was also no consistent relationship between tidal stage and vertical position of larvae (Fig. 2). This was especially evident during cruises 84-9-1 and 85-9-1 when red drum larvae showed the same general pattern in vertical distribution under the opposite stage of the tide.

Moonlight intensity as influenced by moon phase, time of moonrise, and presence/absence of cloud cover did not appear to explain similarities or differences among cruises in nighttime vertical distribution of red drum larvae. Cruises 84-9-2, 85-9-1, and 85-10 were all conducted within 2 to 3 days of the new moon, i.e., when moonlight was at a minimum. Cruises 84-9-1 and 84-10-1 were both conducted 2 to 3 days after the full moon, on cloudless nights with moonrise occurring early in the evening, i.e., when moonlight was near maximum.

The vertical distribution of prey microzooplankton, based on a single collection per depth, was compared with the depth of maximum abundance of red drum larvae at the offshore location (Table 4). Microzooplankton were grouped into three categories based on examination of larval gut contents, net-caught zooplankton, and statistical comparisons of diet and prey availability

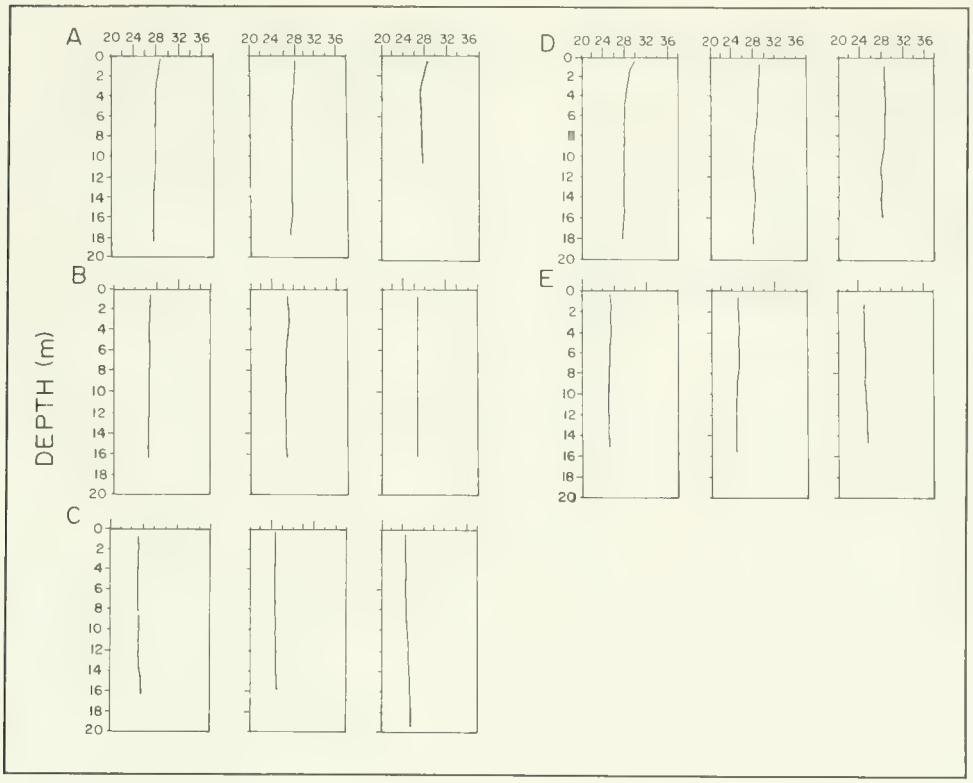

Figure 3
Vertical profiles of temperature (°C, solid line in each plot) and salinity (ppt, dotted line in each plot) during afternoon (left plot), night (center plot), and morning (right plot) sampling periods from cruises: (A) 84-9-1, (B) 84-9-2, (C) 84-10-1, (D) 85-9-1, (E) 85-10.

Table 4
Density of prey microzooplankton (n/L) at three sampling depths and time periods (afternoon, night, and morning) during five cruises in offshore waters. Asterisks indicate depth of highest observed red drum density for that time period. A = density of "preferred" prey; B = density of crustacean nauplii; C = density of total prey zooplankton in the size range 63–230μ maximum width (excluding appendages).

	Afternoon			Night			Morning		
Depth	A	B	C	A	B	C	A	B	C
Cruise 84-9-1									
1	7	81	216*	2	109	189	1	53	97*
5	11	133	275	5	187	313*	1	57	104
11	4	67	91	6	113	172	8	127	215
Cruise 84-9-2									
1	24	44	268	32	97	258	14	137	194
5	22	123	352*	27	139	298	16	118	263*
12	23	61	370	24	79	168*	10	780	182
Cruise 84-10-1									
1	—	—	115	—	—	103	—	—	101*
5	—	—	115	—	—	126	—	—	133
12 (16)	—	—	77*	—	—	186*	—	—	303*
Cruise 85-9-1									
1	10	38	84*	30	75	209	5	53	88
5	23	59	178	21	115	274*	17	90	181*
11	7	71	129	20	86	198	20	60	180
Cruise 85-10									
1	<1	22	72	<1	8	22	<1	22	62*
5	1	36	79*	2	12	45	0	18	46
12 (11)	0.6	23	83	3	27	159*	6	17	128

(Lyczkowski-Shultz et al. 1988). Results of these analyses led to the separation of red drum larvae into three size categories: <2mm, >2 to ⩽4mm, and >4mm, based on diet composition. Column A in Table 4, "preferred" prey, is the combined observed density, from field collections, of those taxa of calanoid and cyclopoid copepods found to most uniquely describe the diet of larvae of the size indicated by the mean lengths listed in Table 3. Crustacean nauplii, column B in Table 4, were the most ubiquitous prey found in red drum larvae of all sizes, and column C is the density of all potential prey items within the size range 63–230μ, i.e., the total size range of prey found to be ingested by red drum larvae.

In only 6 of 15 vertical data sets did the depth of maximum abundance of larvae coincide with the depth of maximum abundance of their prey. Of the 10 daytime vertical data sets when red drum larvae were most likely to be feeding (Lyczkowski-Shultz et al. 1988), the depth of maximum abundance of red drum larvae coincided with the depth of maximum abundance of their prey in only three instances. In one of those instances, the morning sampling period of cruise 84-10-1, red drum larvae were equally abundant at the depths of lowest and highest observed microzooplankton densities.

Discussion

Red drum larvae ranging in mean size from 1.7 to 5.0 mm were vertically stratified in waters of less than 25 m of the northcentral Gulf of Mexico. Larvae were most frequently found to be concentrated higher in the water column during the day than at night in vertically well-mixed coastal and inner shelf waters. The lack of a consistent correspondance between depth of maximum larval red drum abundance and depth of maximum prey microzooplankton abundance was not unexpected since, in general, high prey densities (>100 organisms/L) were observed throughout the water column. Brewer and Kleppel (1986) likewise found no correspondance between prey densities and the daytime vertical distribution of northern anchovy and white croaker larvae. The time lag (2–3 hours) between the collection of ichthyoplankton and zooplankton samples may have affected our results if the spatial coincidence of larvae and prey occurred over a shorter time interval than the interval between samples.

It is feasible to assume that red drum larvae maintain this pattern of vertical distribution by responding to diel changes in illumination. In their recent review, Neilson and Perry (1990) concluded that light is important in mediating diel vertical migration in many fishes throughout ontogeny. Diel variations in the distribution patterns of young fishes are associated with activity, phototaxis, and brightness discrimination (Blaxter 1969). Blaxter (1973) was able to induce vertical migration in herring and plaice larvae by varying ambient light levels in the laboratory or by exposing larvae to natural conditions of dawn and dusk. We have observed that 3-5 day-old red drum larvae in the laboratory are positively phototactic and tend to concentrate at the very surface of 4 L rearing containers with artifical lighting directly overhead. Larvae were not observed under dark conditions. The range in vertical movement, 5–12 m, required to maintain the diel distribution pattern observed in this study is theoretically possible if the swimming capabilities of 2–5 mm drum larvae are similar to those of other fish larvae, i.e., with cruising speeds of 2–3 body lengths per second (Blaxter 1969, Theilacker and Dorsey 1980). The role of the swimbladder, clearly visible in red drum larvae by at least 2 mm, in "depth holding" (Blaxter 1986) is not known. A comprehensive explanation of how red drum larvae maintain vertical position in the shallow depths of their early nursery grounds requires a more thorough knowledge of early sensory and locomotor capabilities in this species.

The pattern of diel vertical distribution displayed by red drum larvae, implying nocturnal descent, has been termed "reverse diel vertical migration" and has been observed by various workers (Wood 1971, Richards and Kendall 1973, Ohman et al. 1983, Kuwahara and Suzuki 1984, Boehlert et al. 1985, Yamashita et al. 1985, Leis 1986, Sogard et al. 1987). From their review of the literature on vertical migration among fishes, Neilson and Perry (1990) found this pattern to be less common than nocturnal ascent, often associated with similiar movements of prey species, and implicated in reducing predation pressure. Yamashita et al. (1985) attributed this distribution pattern among Japanese sand lance larvae to daytime feeding activity in the upper levels of the water column. The authors suggested that when feeding stops after dark, larvae become relatively inactive and gradually sink to greater depths; with the return of daylight, feeding resumes and larvae move upward.

Activity levels among fish larvae are associated with diurnal light changes and phototaxis (Blaxter 1969). The threshold light intensity found to initiate vertical movement of herring and plaice larvae in the laboratory was similiar to the light threshold for feeding (Blaxter 1986). It would be advantageous for larvae such as red drum living in turbid coastal waters to move into more brightly illuminated levels to feed, given the poor visual acuity and limited retinomotor response capabilities (light/dark adaptation) found in the early larvae of most marine fishes (Blaxter 1969).

Prior to this study, vertical distribution of red drum larvae in the Gulf of Mexico had only been described for estuarine/bay systems. Peters and McMichael (1987) never found red drum larvae at the surface during daytime hours in 1 m plankton net collections in Tampa Bay, Florida, where red drum larvae were found to be most abundant nearest the bay mouth. Collections at the bay mouth, however, were taken only at night during a flood tide. The most extensive data on vertical distribution of red drum larvae comes from Aransas Pass tidal inlet on the southern Texas coast where vertical position appears to be influenced by direction of tidal flow (Holt et al. 1989). Further observations and data indicate that high surface densities are generally associated with flooding conditions and/or oceanic water, while high bottom densities occur during ebbing conditions and/or in bay water (S.A. Holt, Mar. Sci. Inst., Univ. Texas at Austin, Port Aransas, TX 78373, pers. commun. Aug. 1990). Tides along the south Texas coast are principally diurnal, and during the red drum spawning season, the flood tide generally occurs at night while the ebb tide occurs during the day.

The relative proportion of the larval red drum population occurring below maximum sampling depths during our study is unknown, but presumed to be small (Comyns et al. 1991). Observations taken during a yearlong survey of Mississippi Sound and adjacent coastal

waters also suggest that red drum larvae, at least during daytime and under flooding conditions, do not occur in large numbers in nearbottom waters of the study area (Lyczkowski-Shultz and Richardson, unpubl. data). Monthly daytime plankton collections were taken from November 1979 to October 1980 at 16 sites inside Mississippi Sound (mean depth 3.9 m), in three tidal passes (mean depth 7.2 m), and at two sites outside the Sound located 7.4 km south of Horn and Petit Bois Islands (mean depth 15.6 m). At each location two depth strata, surface to midwater and midwater to within 0.5 m of the bottom, were sampled separately with stepped oblique hauls of an opening/closing meter net (Lyczkowski-Shultz et al. 1990). Red drum larvae ranging in size from 2.0 to 8.5 mm from 88 collections at all sampling sites combined were more than twice as abundant in the upper half of the water column as in the lower half. This difference was even more pronounced at the two sites outside the Sound where the mean density of larvae (number/100 m^3) was 12.3 in the surface stratum and 4.0 in the bottom stratum. Unlike red drum larvae, the larvae of Atlantic croaker *Micropogonias undulatus* and spotted seatrout *Cynoscion nebulosus* from this same series of collections were more than twice as abundant in the lower half of the water column as in the upper half.

Although the Mississippi Sound and adjacent waters survey was not designed to investigate the role of tide on the distribution of red drum larvae, data from the three barrier island pass stations did tend to support the Aransas Pass inlet observations. Ebbing flow prevailed during sampling at the pass stations only twice during the months when red drum larvae were collected (September and October), and the only instance when drum larvae were more abundant in nearbottom (9 larvae/100 m^3) than in surface waters (0 larvae) occurred during one of those ebb tide collections in Petit Bois Pass. The density of red drum larvae at the offshore station directly south of this pass and under the same ebbing tide, however, was almost three times higher in the surface stratum than in the nearbottom stratum. Our observations from coastal and inner shelf waters during 1984 and 1985 also indicate that tidal stage has little influence on vertical position of red drum in offshore waters.

The vertical distribution of larvae found on cruise 84-10-1 was the only data set that deviated from this generalized pattern. Larvae were concentrated at 12 m during both afternoon and night sampling periods. On the morning of the second day, mean density at 1 and 16 m was the same, suggesting that only a portion of the larval red drum population had moved upward or that the population was still in the process of moving upward. Collections during this cruise contained many large larvae (>4.0 mm) and the night-to-day catch ratio indicated that twice as many larvae were caught during nightime as in daytime collections. Gear avoidance alone does not explain the absence of larvae at 1 and/or 5 m early in the cruise. The catch ratio for cruise 85-9-1, when larvae >4.0 mm were numerous in collections (Table 3), was 0.2, indicating that more larvae were captured in the daytime.

Local conditions in biological and physical environments can modify diel vertical migration patterns among fish larvae (Neilson and Perry 1990). The "anomalous," deeper daytime distribution of red drum larvae early in cruise 84-10-1 may have been related to local environmental conditions. There are no data on which to assess the influence of predator distributions during this study, and there was no apparent coupling between red drum larvae and their prey. Variations in tidal phase or times of sunrise and sunset do not account for the different pattern observed during cruise 84-10-1. Tidal phase was about the same during all three cruises in 1984 (Fig. 2), and the differences in time of sunrise and sunset between sampling dates in September and October were small, only 17 and 36 minutes, respectively. Temperature and salinity profiles during this cruise were indicative of a homogeneous water column.

Meterological conditions may have been in part responsible for the distribution pattern observed during cruise 84-10-1. On both the day preceding and the first day of this cruise, skies were overcast and rainy with winds in excess of 15 knots; whereas on the morning of the second day, and during all other cruises of our study, skies were clear and winds generally were light. Heath et al. (1988) investigated the effects of sea-surface light intensity and wind stress on the vertical distribution of herring larvae. He found larval aggregation at depth to vary at about the same frequency as light intensity, i.e., diurnally; whereas mean population depth (center of density) was most influenced by wind-induced mixing, with larvae being found deeper in the water column at times of higher wind stress. Weather conditions may also have affected the vertical distribution pattern observed during cruise 84-9-2. Winds during this cruise were light, but for prior days winds had been greater than 10 knots. Although larvae were more abundant higher in the water column in the daytime than at night, the diel changes in maximum abundance extended deeper than in the previous cruise, occurring between 5 and 12 m, instead of 1 and 5 m (Fig. 2B).

Characterization of any dynamic biological process such as vertical migration is constrained by sampling design and gear (Pearre 1979). Plankton nets do not, for example, yield information on whether movement within a population is synchronous or asynchronous, or whether rates of ascent and descent differ among segments of the population. Contradictory observations

or deviations from a proposed pattern can result from sample "snapshots" being taken at different times of an ongoing process. Use of a current drogue as a reference marker for the collection of plankton samples in our study increased the probability of staying with, and repeatedly sampling, a particular patch of red drum larvae. This was clearly the case in cruise 84-9-1, when both larval abundance and size composition remained essentially unchanged throughout the duration of the cruise. Use of a reference marker does not, however, invariably ensure that a particular population will continue to be sampled. During cruise 85-9-1, the change in size composition of larvae in the morning sampling period indicated that a different patch of larvae was being sampled. Nonetheless, a drifting or Lagrangian sampling design would be more likely to yield an accurate description of diel vertical movements than the more typical ichthyoplankton survey design where collections are made at varying times and locations. Sampling designs based on fixed stations are more appropriate for resource surveys when observations from large geographic areas encompassing all or most of a species' spawning grounds are needed to estimate spawner biomass from the abundance of eggs and/or larvae.

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Trophic Relationships within the Antarctic Demersal Fish Community of South Georgia Island

James E. McKenna Jr.

Graduate School of Oceanography, University of Rhode Island
Narragansett, Rhode Island 02882
Present address: Florida Marine Research Institute
100 8th Avenue SE, St. Petersburg, Florida 33701

Abstract.– Knowledge of trophic relationships is vital to understanding any ecological community. The trophic relationships of Antarctic demersal fish are poorly known and have been described quantitatively by only a few researchers.

Gut contents were analyzed on over 300 stomachs from fish collected during the 1987–88 AMLR ground fish survey of South Georgia I., Antarctica. All fish were collected with a bottom trawl during the austral summer. Fifteen species of demersal fish (including those of commercial value) were collected. Similarity analysis was applied to the diet information to describe trophic relationships in the South Georgia community.

The most abundant species of the South Georgia demersal fish community were classified into three groups based on summer diets. The largest group contained species heavily dependent on krill *Euphausia superba*, and included *Champsocephalus gunnari* and *Notothenia rossii*. The second group was comprised of piscivores. Three of the four members of this group (*Dissostichus eleginoides*, *Chaenocephalus aceratus*, and *Pseudochaenichthys georgianus*) are commercially valuable. The food of their prey often consisted of krill. The third group contained a loose association of species which feed on benthic organisms more than did other fish species in the community. *Notothenia gibberifrons* and *Notothenia squamifrons* were the important commercial species in this group.

Krill was found to be the most important prey species to the fish in the South Georgia system. However, based on the analysis of diet overlap, competition appeared to be unimportant in this community during the austral summer.

Selective reduction of populations within the fish community by fishing may have widespread repercussions. Many of the commercially valuable species feed on other fish species which in turn feed on krill or benthic organisms. The relatively simple but highly interconnected food web in the South Georgia system may have a lower potential for fish yield than previously thought.

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The Antarctic ecosystem has been physically isolated from the rest of the world for at least the last 30 million years, since the Drake passage opened as South America moved away from Antarctica (Kennett 1982: 726) and probably longer (Regan 1914). The fish assemblage of this region appears to be the result of evolutionary radiation from a limited fauna that was present in the region when Antarctica separated from Australia (Eastman 1985, Kock 1985b). Over 60% of the species and 90% of the individuals belong to four families in the suborder Notothenioidei, and 95% of the species in this group are endemic to the Antarctic region (DeWitt 1971, Kock 1985b). The four dominant families are the Antarctic cods (Nototheniidae), dragonfish (Bathydraconidae), icefish (Channichthyidae), and spiny plunderfish (Harpagiferidae). These fish are generally sedentary, benthic forms found on the Antarctic continental shelves (Norman 1938). An international fishery has developed for larger members of these families, especially in the region around South Georgia I. (Fig. 1) (Kock 1986).

South Georgia is located just south of the Antarctic Convergence and is surrounded by a narrow, relatively shallow continental shelf. The physical oceanography of the region is very complex (Foster 1984) and may contribute to the high productivity and abundance of krill (Hempel 1985).

There is a high degree of endemism in Antarctic fishes (DeWitt 1971). The assemblage of fish species that has evolved in the Southern Ocean is well adapted to the Antarctic environment (Eastman 1985). However, the fish community in the South Georgia area appears to be changing, possibly in response to the fishing pressure that it has experienced over the past two decades (Kock 1985b and 1986, McKenna and Saila 1991). Exploited South Georgian stocks have been declining since the late 1970s (Kock 1985b and 1986, Gabriel 1987). In the early 1970s, the commercial trawl fishery was supported mostly by the catch of marbled rockcod *Notothenia rossii*, which yielded hundreds of thousands of tons each season (Kock 1986). By 1985, the stock was estimated to be less than 10% of its pristine size (Kock 1985b). The fishery is presently supported by catches of mackerel icefish *Champsocephalus gunnari*, but its decline is also evident (Kock 1986, McKenna and Saila 1989). Abundance estimates of other species in the South Georgia region decreased by as much as two orders of magnitude between 1975–76 and 1980–81 (Kock et al. 1985a).

The community structure has changed with decreases in stock sizes (McKenna and Saila 1991). There has been a significant shift from a community dominated by a few large-bodied species to fewer, mostly small-bodied species with more equitable abundances.

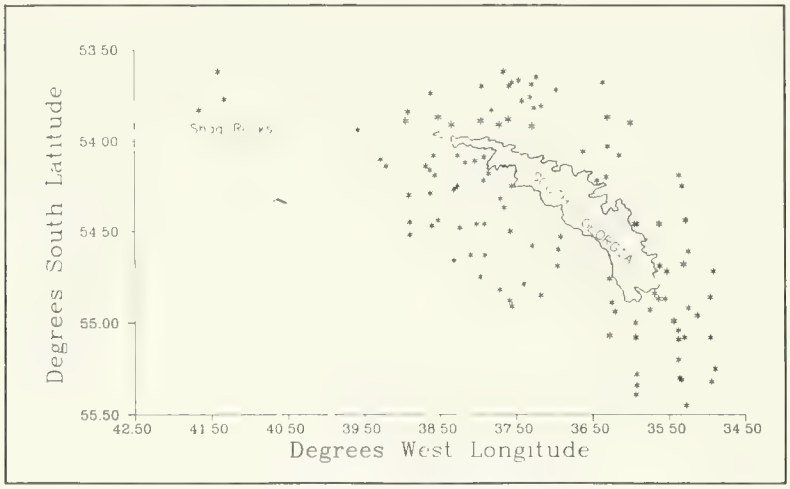

Figure 1
Location of stations sampled around South Georgia I., Antarctica, by the 1987–88 AMLR demersal fish survey.

To effectively manage fish stocks, it is necessary to understand the impact of fishing on the fish community. This includes understanding interspecific relationships among fish and with other organisms in their environment. Knowledge of trophic relationships is necessary to describe these ecological links (Edwards and Bowman 1979, Grosslein et al. 1980, Langton 1983, Sissenwine 1984).

A number of other studies have examined the diets of Antarctic fish (Holloway 1969, Permitin and Tarverdieva 1979, Yukhov 1971, Rakusa-Suszczewski and Piasek 1973, McCleave et al. 1977, Moreno and Osorio 1977). Everson (1984b) reviews the feeding ecology of Antarctic fishes. However, few of these studies have quantitatively measured the interspecific overlap of diets. The most extensive work is that of Targett (1981) who gave a quantitative description of the community structure and trophic relationships of demersal fish around three Antarctic islands. However, his collections were made with a small net (3 m) (not easily compared with those used commercially, (17–18 m)) and only two stations were sampled in the South Georgia I. region late in the autumn of 1975.

Targett's work emphasized the degree of resource partitioning by demersal fish. In general, he found a low degree of overlap in food utilization. In the case of commercial species, however (*Champsocephalus gunnari*, South Georgia icefish *Pseudochaenichthys georgianus*, and painted notie *Nototheniops larseni*), there was a relatively high degree of overlap. This group consists mostly of predators on krill. At one South Georgia station, all fishes preyed on krill.

The present study reports on a quantitative examination of the trophic relationships within the demersal fish community on the continental shelf (~5 km offshore) around South Georgia I.

Methods

The specimens for this study were collected from the research vessel RV *Profesor Siedlecki* using commercial fishing gear, and represent the fishable community that was present during December 1987–January 1988. Fish were collected by 30-minute tows of a P32/36 otter trawl (mouth opening of 17.5 m, 43–52 mm mesh liner) as part of the 1987–88 Antarctic Marine Living Resources (AMLR) survey of the fish stocks around South Georgia I. Successful trawls were made at 108 stations within about 5 km of the island (Fig. 1). These stations were randomly located over the continental shelf within three depth strata (50–150 m, 150–250 m, 250–500 m) (Gabriel 1987, McKenna and Saila 1989). The collection methods are described in detail by McKenna and Saila (1989).

This sampling provided a substantial size range of individuals from the common species and at least a few representatives of most of the rare species (Table 1; McKenna 1990, app. C). A total of 321 stomachs were collected from 15 species of fish. Three of the fifteen species from which stomachs were collected belonged to the icefish family (Channichthyidae; *Champsocephalus gunnari*, black-finned icefish *Chaenocephalus aceratus*, *Pseudochaenichthys georgianus*). Eight species were Antarctic cods (Nototheniidae; *Notothenia rossii*, gray rockcod *Notothenia squamifrons*, striped rockcod *Pagothenia hansoni*, *Nototheniops larseni*, yellowfin notie *Nototheniops nudifrons*, humped rockcod *Notothenia gibberifrons*, Patagonian rockcod *Patagonothen brevicauda guntheri*, and Patagonian toothfish *Dissostichus eleginoides*). Two species of Bathydraconidae (South Georgia icedragon *Parachaenichthys georgianus*, and bronze icedragon *Psilodraco breviceps*) were represented. The remaining two were members of some of the less-common families of the region (Artedidraconidae: fancy plunderfish *Artedidraco mirus*, Mureanolepididae: smalleye morey cod *Muraenolepis microps*.

Length (TL and SL) and weight measurements were taken for fish from each trawl. A stomach index value was also recorded for each fish. This index ranged from zero (empty stomachs) to five (full stomach). Individuals with a stomach index (Permitin and Tarverdieva 1979)

Table 1

Number of stomachs from each fish species collected at South Georgia I., used in diet analyses. n = number of stomachs which contained identifiable prey. Pooled n category = number of replicates used in the community-wide cluster analysis. # = number of stomachs used in the determination of numerical abundance of prey items.

		Number of stomachs					
		n			Pooled n		
Fish species	Species code	#	Wet wt.	Dry wt.	#	Dry wt.	Empty
Artedidraco mirus	ARTE	4	4	4	4	4	1
Chaenocephalus aceratus	ACER	19	19	19	7	7	16
Champsocephalus gunnari	GUNN	41	43	41	15	15	2
Dissosticus eleginoides	ELEG	50	50	50	18	18	0
Muraenolepis microps	MICR	6	6	6	2	2	0
Notothenia gibberifrons	GIBB	22	23	21	8	7	0
Notothenia rossii	ROSS	25	25	25	9	9	1
Notothenia squamifrons	SQUA	13	13	13	5	5	0
Nototheniops larseni	LARS	7	8	7	3	3	3
Nototheniops nudifrons	NUDI	12	14	12	4	4	0
Pagothenia hansoni	HANS	9	9	9	3	3	0
Parachaenichthys georgianus	PARA	9	9	9	3	3	0
Patagonothen brevicauda	GUNT	8	10	7	4	3	0
Pseudochaenichthys georgianus	PSEU	27	27	27	9	9	7
Psilodraco breviceps	PSIL	3	3	3	3	3	0

greater than zero were selected arbitrarily from the catch for gut content analysis. The sex of each fish was also noted. These data were recorded and the stomach was assigned an identification number for correlation with station information.

Stomachs were removed, taking care to prevent loss of any contents. Each stomach was preserved by injection with 10% formalin and wrapped in gauze or paper towels. Large stomachs were soaked in a 10% formalin solution for at least 24 hours. Stomachs were sealed in plastic ziplock bags and stored until they could be examined.

Examination of stomach contents

In the laboratory, the weights of all fish and stomach contents were measured to within 0.001g on an electronic balance. Objects weighing more than 160g were measured on a triple-beam balance. Before contents were removed from the stomach, the total formalin-preserved wet weight was measured. The stomach was then opened with a longitudinal incision through the stomach lining from esophagus to intestine. The contents were removed and sieved through a 0.5mm mesh screen. Wet weight of the empty stomach lining was then measured. This allowed back-calculation of the wet weight of unidentifiable material (GORP) by the difference between total wet weight and the sum of the weights of the separate, identifiable items plus stomach lining. Empty stomachs and those containing only unidentifiable material were not used in the analysis of similarity.

Items remaining on the sieve screen were sorted into general taxonomic groups (e.g., fish, amphipod, isopod) and then identified to family or species where possible. Each group was enumerated and weighed. Specimens were then placed in a drying oven at 60°C and dried to constant weight.

Analysis of the diet data

Frequency of occurrence and dietary coefficients (Linkowski et al. 1983) were determined as simple measures of the importance of each potential prey item in the diet of each species (Table 2). To remove the biases due to varying stomach size and total number of items contained in each stomach, all diet data were converted to percent composition. Percent composition of the diet was determined for each stomach based on numerical abundance, wet weight, and dry weight of the prey items. Results refer to the use of percent composition by dry weight unless stated otherwise. Average percent composition of the diet was then calculated for each of the 15 species of fish for which stomachs had been collected (Table 3). Only stomachs which contained identifiable prey items were included in the diet analysis.

Table 2

Frequency of occurrence (%), dietary coefficient (Q), and diversity values for the diets of 15 Antarctic demersal fish species collected off South Georgia I. SPP = fish species code (see Table 1 for key to specific identification); %f = percent frequency of occurrence; Q = average number of prey × average dry weight of prey; H = Shannon-Wiener diversity index using average percent composition of the diet of each species; var(H) = variance of Shannon-Wiener index (Hutcheson 1970).

SPP:	ACER	ARTE	ELEG	GIBB	GUNN	GUNT	HANS	LARS	MICR	NUDI	PARA	PSEU	PSIL	ROSS	SQUA
Fish															
%f	84.62	0.00	96.00	0.00	0.00	37.50	11.11	0.00	33.33	0.00	77.78	62.96	0.0	52.00	0.00
Q	6.92	0.00	7.65	0.00	0.00	0.48	0.00	0.00	0.09	0.00	1.91	6.65	0.0	7.27	0.00
Krill															
%f	15.38	25.00	18.00	50.00	100.00	100.00	100.00	42.86	16.67	83.33	22.22	59.26	100.0	76.00	30.77
Q	0.91	0.01	0.01	0.08	58.89	15.01	7.96	0.07	0.00	0.19	0.13	64.11	1.8	165.14	0.00
Tunicate															
%f	0.00	0.00	0.00	31.82	0.00	0.00	11.11	28.57	16.67	0.00	0.00	3.70	0.0	44.00	84.62
Q	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.17	5.73
Amphipod															
%f	0.00	25.00	2.00	68.18	0.00	0.00	11.11	28.57	50.00	25.00	0.00	0.00	0.0	32.00	61.54
Q	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.02	0.01	0.02	0.00	0.00	0.0	5.12	0.01
Isopod															
%f	0.00	50.00	0.00	36.36	0.00	0.00	11.11	0.00	0.00	8.33	0.00	0.00	0.0	20.00	38.46
Q	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.00	0.00
Polychaete															
%f	0.00	50.00	0.00	86.36	2.44	0.00	0.00	0.00	33.33	16.67	0.00	0.00	0.0	8.00	23.08
Q	0.00	0.00	0.00	6.56	0.00	0.00	0.00	0.00	0.01	0.04	0.00	0.00	0.0	0.03	0.01
Shrimp															
%f	15.38	0.00	6.00	9.09	0.00	0.00	0.00	0.00	16.67	0.00	66.67	0.00	0.0	28.00	0.00
Q	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.09	0.00	0.0	0.19	0.00
Echiura															
%f	0.00	0.00	0.00	22.73	0.00	0.00	0.00	0.00	16.67	8.33	0.00	0.00	0.0	0.00	7.69
Q	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.00	0.00
Gastropod															
%f	0.00	0.00	0.00	45.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	8.00	7.69
Q	0.00	0.00	0.00	36.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.00	0.00
Rocks															
%f	0.00	0.00	4.00	13.64	0.00	0.00	0.00	0.00	33.33	16.67	0.00	0.00	0.0	0.00	7.69
Q	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0.00	0.00
Diversity															
H	0.988	1.464	0.198	1.772	0.00	0.573	0.389	1.296	1.701	1.148	0.96	0.677	0.0	1.306	1.613
var(H)	0.0107	0.0018	0.0042	0.0143	0.00	0.0022	0.0092	0.0019	0.004	0.0086	0.0028	0.0004	0.0	0.0101	0.017

Similarity analysis was used to classify fish species into distinct trophic groups based on their diets. Two techniques were used. The first, based on the work of Smith (1985), generated a matrix of similarity coefficients and associated variances for each pair of species being compared. Similarity was measured with the proportional similarity coefficient (PS) for each pair of fish species being compared. This analysis was based on the average percent composition for each species.

The second method applied cluster analysis to these data. I used the clustering methods of Nemec and Brinkhurst (1988), which use a bootstrap technique applied to replicate samples to determine the significance of clusters. The Bray-Curtis similarity coefficient was used and, where replicates were available, significance was tested using 50 bootstrap simulations. For each species, a separate cluster analysis was performed to determine if there were significant intraspecific subgroups by size, sex, or depth of habitat (McKenna 1990, app. D). Although the variability in diet of each species was obvious, no significant subgroups were identified.

Cluster analysis was then applied to examine the structure of the community. There is virtually no spatial structure to the South Georgia fish community at this season (McKenna 1990:178–251) and, since no significant intraspecific structure was found, each stomach examined was used as a replicate sample of the diet of the predator species (Table 1). These data were used in the SIGTREE cluster analysis program (Nemec and Brinkhurst 1988). Due to a limitation of the program (a maximum of 110 observations [sum of replicates per species] are allowed), the data were pooled into groups of three and averaged to reduce the number of observations from 264 to 97 (Table 1).

Table 3

Average percentages of total diet contributed by each prey species for 15 Antarctic demersal fish species collected around South Georgia I. Asterisk (*) = prey item accounted for <0.1% of the diet. See Table 1 for key to species code identifications.

Prey item	ACER	ARTE	ELEG	GIBB	GUNN	GUNT	HANS	LARS	MICR	NUDI	PARA	PSEU	PSIL	ROSS	SQUA
Based on numerical abundance of prey items															
Fish	59.6	0.0	83.6	0.0	0.0	15.5	2.8	0.0	13.9	0.0	39.1	43.9	0.0	14.2	*
Krill	18.5	15.0	11.1	5.2	99.3	84.5	86.1	33.3	4.2	65.3	22.2	56.1	100.0	64.6	5.6
Tunicate	0.0	0.0	0.0	5.1	0.0	0.0	5.6	16.7	8.3	0.0	0.0	*	0.0	9.5	47.5
Amphipod	0.0	16.7	*	10.9	0.0	0.0	2.8	38.9	20.8	10.1	0.0	0.0	0.0	3.6	32.8
Isopod	0.0	30.0	0.0	1.4	0.0	0.0	2.8	0.0	0.0	1.4	0.0	0.0	0.0	*	5.0
Polychaete	0.0	13.3	0.0	52.3	0.6	0.0	0.0	0.0	16.7	11.4	0.0	0.0	0.0	0.6	3.9
Shrimp	16.2	0.0	3.1	*	0.0	0.0	0.0	0.0	5.6	0.0	38.7	0.0	0.0	5.4	0.0
Echiura	0.0	0.0	0.0	3.8	0.0	0.0	0.0	0.0	16.7	8.3	0.0	0.0	0.0	0.0	*
Ctenophora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2
Cumacid	0.0	0.0	0.0	4.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gastropod	0.0	0.0	0.0	15.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	*
Hydroid	1.0	0.0	0.0	0.0	0.0	0.0	0.0	11.1	0.0	0.0	0.0	0.0	0.0	*	0.0
Crust. spp.	4.8	25.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rocks	0.0	0.0	1.7	*	0.0	0.0	0.0	0.0	13.9	3.5	0.0	0.0	0.0	0.0	2.2
Based on wet weight of prey items															
GORP	18.8	48.0	6.1	41.5	12.4	42.7	26.0	34.7	30.9	26.9	9.6	14.3	6.6	21.2	19.6
Fish	60.3	0.0	88.7	0.0	0.0	10.3	0.0	0.0	15.8	0.0	49.9	50.0	0.0	27.1	0.0
Krill	7.9	16.5	4.7	1.4	85.4	46.9	71.2	31.9	2.1	49.8	21.2	35.5	93.4	38.6	1.5
Tunicate	0.0	0.0	0.0	4.9	0.0	0.0	2.3	12.1	3.1	0.0	0.0	*	0.0	7.7	66.6
Amphipod	0.0	2.6	*	2.1	0.0	0.0	*	8.7	5.0	4.7	0.0	0.0	0.0	1.7	3.0
Isopod	0.0	27.3	0.0	*	0.0	0.0	*	0.0	0.0	*	0.0	0.0	0.0	*	2.0
Polychaete	8.0	4.4	0.0	28.6	*	0.0	0.0	0.0	25.1	10.6	0.0	0.0	0.0	*	1.7
Shrimp	0.1	0.0	*	3.3	0.0	0.0	0.0	0.0	1.2	0.0	19.3	0.0	0.0	2.0	0.0
Echiura	0.0	0.0	0.0	4.3	0.0	0.0	0.0	0.0	15.5	6.9	0.0	0.0	0.0	0.0	4.2
Gastropod	0.0	0.0	0.0	12.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	*
Hydroid	*	0.0	0.0	0.0	0.0	0.0	0.0	12.5	0.0	0.0	0.0	0.0	0.0	*	0.0
Based on dry weight of prey items															
Fish	63.4	0.0	95.2	0.0	0.0	37.8	4.4	0.0	25.5	0.0	58.6	58.9	0.0	36.1	*
Krill	10.3	18.5	4.3	4.8	99.6	62.2	90.7	33.3	2.0	62.1	21.9	41.0	100.0	45.5	3.8
Tunicate	0.0	0.0	0.0	7.5	0.0	0.0	3.6	22.8	9.5	0.0	0.0	*	0.0	6.2	48.8
Amphipod	0.0	3.2	*	5.3	0.0	0.0	*	32.8	9.6	12.7	0.0	0.0	0.0	4.0	10.0
Isopod	0.0	30.2	0.0	1.5	0.0	0.0	1.2	0.0	0.0	*	0.0	0.0	0.0	*	9.0
Polychaete	0.0	23.1	0.0	48.4	*	0.0	0.0	0.0	31.1	12.2	0.0	0.0	0.0	*	2.2
Shrimp	17.5	0.0	*	4.5	0.0	0.0	0.0	0.0	5.6	0.0	19.1	0.0	0.0	3.2	0.0
Echiura	0.0	0.0	0.0	5.4	0.0	0.0	0.0	0.0	16.7	8.3	0.0	0.0	0.0	0.0	5.1
Gastropod	0.0	0.0	0.0	14.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	5.7
Hydroid	*	0.0	0.0	0.0	0.0	0.0	0.0	11.1	0.0	0.0	0.0	0.0	0.0	*	0.0
Crust. spp.	4.8	25.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rocks	0.0	0.0	*	3.0	0.0	0.0	0.0	0.0	*	4.2	0.0	0.0	0.0	0.0	6.9
Other	5.0	0.0	1.0	4.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	8.0

Results

Krill and fish were the dominant items in the diets of these fish (Table 2). In addition to these items, 26 types of invertebrates and plant material were represented in the guts (Sponges, Ctenophores, Cnidarians, Nemeratines, Nematodes, Bivalves, Cephalopods, Picnogonids, Cumacids, Tanaids, Copepods, Mysids, Bryozoans, and Echinoderms accounted for less than 1% of the diet). Of the 321 stomachs examined, 26 were discarded because they were not properly preserved, 30 were empty, and 13 contained only unidentifiable material. The highest proportion of unidentifiable material (among the stomachs used in the similarity anaysis) was 48% (on a wet weight basis) and occurred in *Artedidraco mirus* (Table 3). The ratio of dry weight to wet weight of unidentifiable material averaged 22%. This is within the range of values for identifiable prey items in the diets and was most similar to the same ratio for fish (Table 4). Despite the problems of differential digestion, it was assumed that the proportions of identifiable material were accurate representations of the diet of these fish.

Every species examined ate some krill (Table 2). However, most pairwise comparisons of species diets

Table 4

Dry- to wet-weight ratios for the most common prey items in the diets of 15 species of Antarctic demersal fish.

Prey taxon	Identified species	Dry:Wet (%)
Amphipod	*Vibilia antarctica*	18.62
	Parathemisto gaudichaudii?	
	Hyperiidae	
	Hyperoche medusarum?	
Echirua		24.01
Fish	*Chaenocephalus aceratus*?	23.79
	Artedidraco mirus?	
	Dissosticus eleginoides	
	Champsocephalus gunnari	
	Patagonothen brevicauda?	
	Pagothenia hansoni	
	Nototheniops larseni	
	Muraenolepis microps	
	Nototheniops nudifrons?	
	Parachaenichthys georgianus	
	Trematomus spp.?	
Gastropod	*Atlantica* spp.?	12.66
Isopod	*Arcturus* spp.?	15.42
Krill	*Euphausia superba*	17.76
Polychaete	*Sternapsis* spp.?	17.58
	Maldanidae	
	Lumbrineridae?	
	Terribellidae?	
	Philodocidae?	
Shrimp	*Crangon antarcticus*?	18.42
Tunicate		9.76
GORP		22.06

showed less than 50% overlap (Tables 5, 6), suggesting that in most cases resource partitioning was occurring. This is supported by the cluster analysis which showed that there was more than one significant cluster (Figs. 2, 3). The species or groups of species distinguished by the cluster analysis were feeding on different sets of prey. There were three groups of species in the community: fish-eaters, krill-eaters, and benthic invertebrates feeders.

Fish-eaters

The four members of the fish-eating group included most of the large carnivorous species in the region. The diets of *C. aceratus* and *Parachaenichthys georgianus* showed the greatest similarity (Figs. 2, 3) within the fish-eating group and overlapped by 78% (Table 6). They fed predominantly on fish, but each species also consumed roughly similar proportions of krill *Euphausia superba* and shrimp *Notocrangon antarcticus* (Table 3). Although little is known about the life history of *Parachaenichthys georgianus*, both it and *C. aceratus* appear to be epibenthic in their behavior.

Chaenocephalus aceratus is the largest species of icefish found in the South Georgia region, growing up to 75 cm (Fischer and Hureau 1985). It is an ambush predator (Kock 1985b). Heavily calloused pelvic fins of older individuals indicate that it spends much of its time sitting on the bottom. Fish prey included *Parachaenichthys georgianus* and *N. larseni*, which were as much as 58% of its body size (TL).

Table 5

Proportional prey overlap in the diets of 15 Antarctic demersal fish species collected off South Georgia I., based on the numerical abundance of prey items in each diet. Proportional similarity coefficient values are given in the upper subdiagonal of the matrix. Variance of the proportional similarity coefficient values are given in the lower subdiagonal of the matrix. Values of ≥0.5 have been underlined.

	ACER	ARTE	ELEG	GIBB	GUNN	GUNT	HANS	LARS	MICR	NUDI	PARA	PSEU	PSIL	ROSS	SQUA
ACER	–	0.2026	0.8118	0.0594	0.2043	0.2864	0.2321	0.2148	0.2362	0.2043	0.6687	0.6430	0.2043	0.4170	0.0614
ARTE	0.1773	–	0.1250	0.3013	0.1567	0.1500	0.2056	0.3167	0.3417	0.3785	0.1500	0.1500	0.1500	0.2420	0.3559
ELEG	0.3547	0.1094	–	0.0672	0.1200	0.2021	0.1528	0.1250	0.2372	0.1433	0.5440	0.5587	0.1200	0.3117	0.0847
GIBB	0.0559	0.2553	0.0633	–	0.0638	0.0571	0.1557	0.2089	0.4070	0.3248	0.0594	0.0573	0.0571	0.2101	0.3062
GUNN	0.1626	0.1342	0.1056	0.0605	–	0.9179	0.8611	0.4286	0.0484	0.6601	0.2222	0.5612	0.9922	0.5853	0.0681
GUNT	0.2379	0.1275	0.1810	0.0538	0.0754	–	0.8889	0.4286	0.1238	0.6534	0.3043	0.6433	0.9179	0.6607	0.0614
HANS	0.1896	0.1800	0.1364	0.1435	0.1196	0.0988	–	0.5120	0.1529	0.6951	0.2500	0.5892	0.8611	0.6970	0.1726
LARS	0.1687	0.2164	0.1094	0.1653	0.2449	0.2449	0.3213	–	0.3333	0.5296	0.2222	0.4288	0.4286	0.6104	0.4051
MICR	0.1804	0.2500	0.2014	0.3241	0.0466	0.1153	0.1388	0.2222	–	0.3743	0.2362	0.1808	0.0417	0.4043	0.3767
NUDI	0.1626	0.3038	0.1228	0.2696	0.2331	0.2265	0.2490	0.3357	0.2619	–	0.2222	0.5612	0.6534	0.6706	0.2510
PARA	0.4388	0.1275	0.3679	0.0559	0.1728	0.2482	0.1999	0.1728	0.1804	0.1728		0.6129	0.2222	0.4334	0.0614
PSEU	0.4088	0.1275	0.3518	0.0540	0.2463	0.3216	0.2733	0.2451	0.1482	0.2463	0.2373	–	0.5612	0.7148	0.0616
PSIL	0.1626	0.1275	0.1056	0.0538	0.0077	0.0754	0.1196	0.2449	0.0400	0.2265	0.1728	0.2463	–	0.5786	0.0614
ROSS	0.3300	0.2110	0.2631	0.1878	0.2505	0.3192	0.3415	0.3937	0.2950	0.2209	0.3394	0.3761	0.2438	–	0.2574
SQUA	0.0576	0.2923	0.0804	0.2484	0.0643	0.0576	0.1565	0.3205	0.2977	0.2193	0.0576	0.0578	0.0576	0.2152	–

Table 6

Proportional prey overlap in the diets of 15 Antarctic demersal fish species collected off South Georgia I., based on the dry-weight abundance of prey items in each species diet. Proportional similarity coefficient values are given in the upper subdiagonal of the matrix. Variance of the proportional similarity coefficient values are given in the lower subdiagonal of the matrix. Values of ≥0.5 have been underlined.

	ACER	ARTE	ELEG	GIBB	GUNN	GUNT	HANS	LARS	MICR	NUDI	PARA	PSEU	PSIL	ROSS	SQUA
ACER	—	0.1665	0.7514	0.0924	0.1139	0.3723	0.1575	0.1145	0.3311	0.1139	0.7878	0.7033	0.1139	0.4819	0.0458
ARTE	0.1388	—	0.0460	0.3253	0.1862	0.1846	0.1980	0.2166	0.2827	0.3434	0.1846	0.1846	0.1846	0.2229	0.2043
ELEG	0.2576	0.0439	—	0.0514	0.0459	0.3043	0.0896	0.0460	0.2798	0.0468	0.6373	0.6353	0.0459	0.3833	0.0444
GIBB	0.0839	0.2522	0.0488	—	0.0491	0.0475	0.0966	0.1757	0.5578	0.3111	0.0930	0.0482	0.0475	0.1918	0.3132
GUNN	0.1009	0.1521	0.0438	0.0468	—	0.7416	0.9073	0.4286	0.0213	0.6224	0.2194	0.4099	0.9961	0.4929	0.0451
GUNT	0.2926	0.1505	0.2354	0.0452	0.1916	—	0.7852	0.4286	0.2751	0.6208	0.4778	0.6683	0.7416	0.7497	0.0435
HANS	0.1426	0.1637	0.0856	0.0919	0.0841	0.2333	—	0.4661	0.1008	0.6275	0.2630	0.4542	0.9073	0.5799	0.0926
LARS	0.1014	0.1697	0.0439	0.1448	0.2449	0.2449	0.2810	—	0.2107	0.5561	0.2194	0.4106	0.4286	0.5165	0.2948
MICR	0.2215	0.1231	0.2041	0.3968	0.0209	0.1994	0.0938	0.1663	—	0.3212	0.3311	0.2758	0.0197	0.4079	0.2566
NUDI	0.1009	0.2804	0.0446	0.2611	0.2370	0.2354	0.2360	0.3561	0.2656	—	0.2200	0.4099	0.6208	0.5270	0.2170
PARA	0.4035	0.1505	0.2904	0.0845	0.1713	0.3629	0.2130	0.1713	0.2215	0.1716	—	0.8056	0.2194	0.5872	0.0470
PSEU	0.3429	0.1505	0.2858	0.0459	0.2419	0.4335	0.2837	0.2420	0.2001	0.2419	0.1566	—	0.4099	0.7433	0.0442
PSIL	0.1009	0.1505	0.0438	0.0452	0.0039	0.1916	0.0841	0.2449	0.0193	0.2354	0.1713	0.2419	—	0.4913	0.0435
ROSS	0.3335	0.1874	0.2701	0.1687	0.2515	0.4416	0.3245	0.3251	0.3146	0.2544	0.4038	0.4640	0.2499	—	0.1531
SQUA	0.0437	0.1736	0.0425	0.2610	0.0432	0.0416	0.0883	0.2472	0.2233	0.1720	0.0451	0.0423	0.0416	0.1393	—

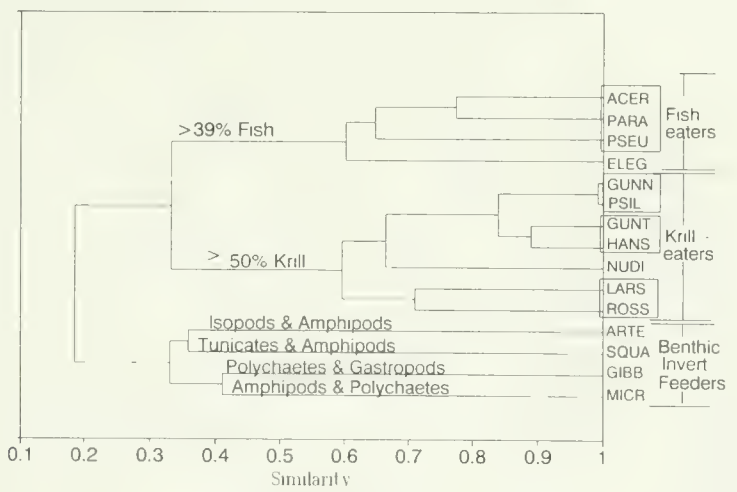

Figure 2

Dendrogram representing the classification of Antarctic demersal fish into trophic groups based on numerical abundance of prey items in their guts. Refer to Table 1 for key to species codes. Species grouped together within a box were identified as having significantly similar diets.

Parachaenichthys georgianus has a scaleless, elongate body. Its mouth is tube-shaped and probably functions like a slurp gun. It may be an ambush predator like the *C. aceratus*. Its diet consisted mainly of fish (59%) and roughly equal proportions of krill and shrimp (Table 3). None of the fish it consumed were identifiable. Its diet overlapped most (80%) with that of the *Pseudochaenichthys georgianus* (Table 6).

Pseudochaenichthys georgianus also preyed heavily on other fish (59%)(Table 3). Like *C. aceratus*, it has a large mouth. However, it tended to feed on smaller fish and more krill than *C. aceratus* and did not eat shrimp. It fed on a variety of other fish species including *N. larseni*, *C. gunnari*, *M. microps*, and *Parachaenichthys georgianus*. Its diet overlapped most (80%) with that of *Parachaenichthys georgianus*.

D. eleginoides is the largest of all Antarctic demersal fish, growing to over 2m, and is an active predator (Fischer and Hureau 1985). It is known to be pelagic during some stages of its life (Fischer and Hureau 1985), but the presence of rocks in a few stomachs indicates that some had been feeding close to the bottom. It fed almost exclusively on fish (97%) (Table 3). Based on identifiable fish in the guts, it preyed on *M. microps*, *N. larseni*, *Parachaenichthys georgianus*, and its own young. Stomachs from this species often contained a single fish that was as much as 53% of the size (TL) of the predator. Its diet overlapped most (75%) with that of *C. aceratus*.

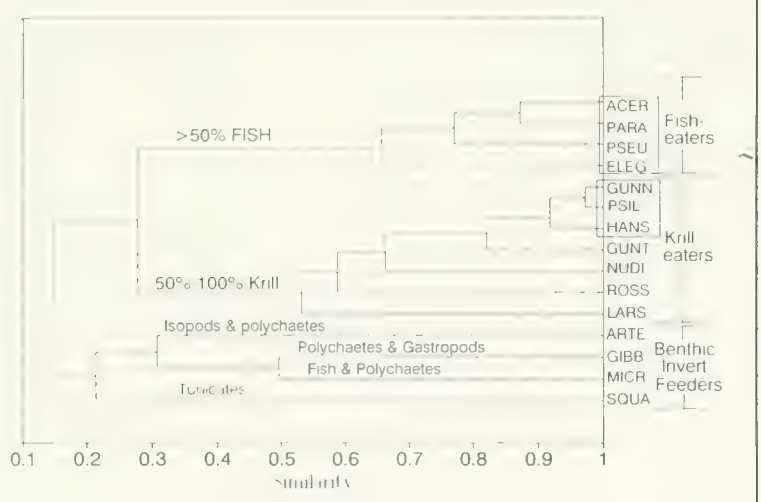

Figure 3

Dendrogram representing the classification of Antarctic demersal fish into trophic groups based on dry weight of their gut contents. Refer to Table 1 for key to species codes. Species grouped together within a box were identified as having significantly similar diets.

Krill-eaters

Seven species were grouped as krill-eaters. The hierarchical cluster analysis places *C. gunnari*, *P. breviceps*, and *P. hansoni* in a single cluster and identifies others within this group as distinct clusters. The cluster analysis arranged these species in order of decreasing proportion of krill in the diet (Fig. 3, from top to bottom). These species are probably more pelagic in nature than other members of the community, with the possible exception of *N. nudifrons* (Permitin and Tarverdiyeva 1972, Targett 1981).

C. gunnari and *P. breviceps* had the most similar diets (Table 6), feeding almost exclusively (>97%) on krill. *Psilodraco breviceps* diet consisted 100% of krill (Table 3), but only three specimens were examined and the true variability of this species' diet may not be accurately represented here.

Champsocephalus gunnari is the most important commercial species around South Georgia (Kock 1986, Gabriel 1987, McKenna and Saila 1989). It leads a more pelagic existence than its local relatives (*C. aceratus*, *P. georgianus*) (Kock 1985b). Its heavy dependence on krill has been documented (Targett 1981, Permitin and Tarverdiyeva 1972, Permitin and Tarverdieva 1979, Tarverdiyeva and Pinskaya 1980, Kock 1981). In this sample, its diet was composed almost entirely (99%) of krill (Table 3).

Little is known about the life history of *P. hansoni*, except for its heavy dependence on krill (Targett 1981). In 1987–88, its diet consisted primarily of krill (91%), but it also fed on fish and tunicates (Table 3). Its diet overlapped those of *C. gunnari* and *P. breviceps* by more than 90% (Table 6).

Patogonothen brevicauda is endemic to a shallow shelf region west of South Georgia known as Shag Rocks. Its diet consisted of 80% krill and 20% fish (Table 3). Its diet overlapped that of four other species (*C. gunnari*, *P. hansoni*, *P. breviceps*, and *N. rossii*) by more than 70%, due to the heavy dependence on krill (Table 6).

Nototheniops nudifrons is thought to be benthic in nature (Targett 1981, Permitin and Tarverdiyeva 1972, Permitin and Tarverdieva 1979). However, in 1987–88, 66% of its diet consisted of krill (Table 3) and the remainder was composed of epibenthic invertebrates. Rocks accounted for about 0.5% of the average dry-weight contents. Its diet overlapped that of four other species (*C. gunnari*, *P. brevicauda*, *P. hansoni*, and *P. breviceps*) by 62% (Table 6).

Notothenia rossii is a large (90 cm) species that was the mainstay of the commercial catch during the early 1970s (Kock 1986). Its diet was diverse, but it was grouped with the krill-eaters because 46% of its food was krill (Table 3). Fish was the second-most-important item in its diet and included *Parachaenichthys georgianus*, *M. microps*, *P. hansoni*, and *N. larseni*. *Notothenia rossii*'s diet overlapped most (74%) with those of *Pseudochaenichthys georgianus* and *P. brevicauda* (Table 6).

Nototheniops larseni is considered to be one of the most pelagically adapted of the nototheniids (Targett 1981). Previous work has shown that its diet is often dominated by krill (Permitin and Tarverdyieva 1972 and 1979, Targett 1981, Daniels 1982). In this study, krill comprised only one-third of its diet, and 56% was pelagic tunicates and amphipods (Table 3). Its diet overlapped that of *N. nudifrons* by 55% (Table 6).

Consumers of benthic invertebrates

All of the members of the 'benthic invertebrate feeders' group had diets which were distinct from one another as well as from members of the other major groups. However, these fish all seemed to be closely associated with the bottom.

Notothenia squamifrons diet was the most unusual of all the species examined. It included a large proportion (49%) of tunicates (salps) (Table 3). The remainder of its diet consisted almost entirely of benthic invertebrates. Krill made up only 4%. The preponderance

of salps is also a feature of the diet of *N. squamifrons* found at Kerguelen I. (Duhamel and Hureau 1985). *Notothenia squamifrons* diet displayed the least amount of overlap of all the species examined. It reached a maximum of 32% when compared with that of *N. gibberifrons* (Table 6).

Polychaetes were a major component (>23%) of the diets of the three remaining species. *Notothenia gibberifrons* is an important commercial species. It was the dominant species (numerically and by biomass) during the 1988–89 AMLR survey of the South Georgia region (McKenna 1989). It is a benthic species, which uses its relatively small, subterminal mouth to 'slurp up' benthic epi- and infauna (Daniels 1982). It had the most diverse diet of the species examined (Table 2); however, over 50% of its diet consisted of polychaetes. The remainder was comprised of invertebrate epifauna and a small amount of krill (5%, Table 3). Its diet overlapped most (56%) with that of *M. microps* (Table 6).

Mureanolepis microps is a scaleless, eel-like species with a diverse diet (Table 2). It was the only 'benthic invertebrate feeder' to eat fish (Table 3). Nine percent of its diet consisted of salps and 2% of krill. The other items in the diet were benthic organisms. Polychaetes were the dominant prey item. Its diet overlapped most (56%) with that of the *N. gibberifrons* (Table 6).

Artedidraco mirus was the smallest species (~8 cm TL) consistently caught in the trawl. Its diet was composed mostly of isopods and polychaetes (Table 3). This species was represented by only four stomachs, which may not accurately display the true diet of this species at South Georgia. The greatest overlap of its diet (34%) occurred with *N. nudifrons* (Table 6).

Discussion

These results support the conclusions of earlier workers, in that the most abundant species (including those of commercial value) of the South Georgia demersal fish community can be classified into three groups based on their summer diets. The largest group contained those fish that depended heavily on krill and included *C. gunnari* and *N. rossii*. Fish-eaters represented a second distinct group. Three of the four members of this group (*D. eleginoides*, *C. aceratus*, and *Pseudochaenichthys georgianus*) are commercially valuable. The third group contained a loose association of species which tended to feed mostly on benthic invertebrates. *Notothenia gibberifrons* and *N. squamifrons* are the commercially important members of this group. *Notothenia gibberifrons* is one of the most abundant species in the region, while *N. squamifrons* is rare on the continental shelf around South Georgia (<500 m) (McKenna and Saila 1989, McKenna 1989).

The fishes at South Georgia were using two different food resources: pelagic organisms (mostly krill) and benthic organisms. The large benthic biomass of the Antarctic appears incapable of supporting a large or diverse fish fauna because most of it is in the form of non-food species (e.g., sponges, sea stars) (Belyaev and Ushakov 1957, Andriashev 1965). This may explain why *N. gibberifrons*, and a few less-common species, were the only fish that depended heavily on benthic organisms. To survive in this environment, these fish have had to diversify their diets and draw upon more prey species than the pelagic fish of the region.

The majority of fish in the vicinity of South Georgia I. relied on the pelagic food resource. The adaptations of many of these basically benthic fishes to pelagic feeding (Nybelin 1947, Permitin 1970, Eastman 1985, Kock 1985b) indicate the relative superiority, in quality and/or availability, of food in the pelagic realm. Krill was the only food resource consumed by all species of Antarctic fish examined in this study. Five of the fifteen species examined relied on krill for greater than 50% of their diet.

There were direct and indirect trophic links between krill and piscivores. All piscivores ate some krill, and most of the identifiable fish that they ate were krill-eaters. However, most of the fish consumed by piscivores in this study were unidentifiable, and a stong link between a piscivore (*N. rossii*) and the benthos (*N. gibberifrons*) has been demonstrated at Kerguelen I. (Linkowski et al. 1983). Thus, the relative magnitudes of links between piscivores and krill or the benthos remain unknown.

Diet overlap and interspecific competition

In paired comparisons, there was at least some overlap in the diets, especially in those species relying heavily on krill. However, in most cases the overlap was less than 50%, indicating that resources were effectively partitioned within the South Georgia community during the austral summer.

Despite the heavy dependence on krill and high overlap (90%) of the diets of a few species, competition is probably not important in the Antarctic demersal fish community during the summer (Targett 1981, Daniels 1982). Competition occurs only when the resource in common use is limiting (Larkin 1963). The availability of krill to Antarctic fish varies (Permitin and Tarverdieva 1979), but whether it is limiting is unknown. In some years, krill is abundant enough to come in contact with the bottom and is then available to even strict benthic feeders like *N. gibberifrons* (Targett 1981).

This study suggests that resources are effectively partitioned in the austral summer. However, the Antarctic undergoes strong seasonal changes, which affect the abundance and availability of krill as well as other aspects of the ecosystem. Krill spawn in summer and the larvae migrate vertically from great depths (>500 m) as they develop over the winter, recruiting to the population the next summer (Marshall 1979). Adult and juvenile krill do most of their growing in summer when they may be superabundant, occurring in dense 'swarms' (Everson 1984a). During the unproductive winter, krill grow little or may even shrink in size (Ikeda and Dixon 1982), but their distribution at that time is poorly known.

The trophic structure of the Antarctic fish community may change in response to these seasonal events. Prey switching and niche shifts offer two mechanisms to deal with these seasonal changes. Although diet diversities were low for South Georgia fishes, all species (with the exception of *P. breviceps*) consumed at least one alternative food resource regularly. This indicates that there is the potential for prey switching according to the availability of the prey resources in the environment. Seasonal prey switching has been inferred from changes in the diets of related species living along the Antarctic Peninsula (Daniels 1982).

Niche shifts may occur to reduce competition at times when krill is limiting. As krill becomes more limiting, behaviorial changes, such as a shift to more specialized feeding on alternative prey or in specific habitats, may occur. To test these hypotheses a seasonal time series of diets and the availability of prey is needed.

Possible effects of commercial fishing

Selective removal of species by fishing will effect the demersal fish community. Prey of removed predators may benefit from reduced predation, as has been suggested for *Champsocephalus gunnari* at Kerguelen I. (Duhamel and Hureau 1985). One competitor may benefit by increased fecundity if the other is removed by fishing (Beddington and May 1982). Competition may be intensified at a lower trophic level if a predator on one species of a competing pair is reduced (Miller and Kerfoot 1987, Abrams 1987, Boisclair and Leggett 1989). If a niche shift had taken place in the past to reduce competition, a species may expand to occupy more of a niche when its competitor is removed (Connell 1980, Beddington and May 1982). However, it is difficult to predict the response of the community without more data on the life histories and seasonal dynamics of these fish and their prey.

Ecological efficiency is another topic to be considered when harvesting an Antarctic community. The South Georgia community is highly productive (Hempel 1985). The diversity of the system is low and the food web is relatively simple (Beddington and May 1982). However, the cost of activity and survival in the Antarctic is high (Hempel 1985) and the loss of energy at each trophic transfer places a limitation on the biomass of fish available for harvest. Many of the commercially valuable species are large piscivores (*Chaenocephalus aceratus*, *Pseudochaenichthys georgianus*, *Dissostichus eleginoides*, *Notothenia rossii*) one or more steps removed from secondary production. The availability of krill to these fish and their prey, and the fish's ability to emphasize krill in their diets, will strongly influence the yield of fish from the South Georgian community.

Conclusions

The most abundant species of the South Georgia demersal fish community were classified into three groups based on their summer diets. Species that depended heavily on krill comprised the largest group, including *Champsocephalus gunnari* and *Notothenia rossii*. The second group was comprised of piscivores. Three of the four members of this group (*Dissostichus eleginoides*, *Chaenocephalus aceratus*, and *Pseudochaenichthys georgianus*) are commercially valuable. The food of their prey often consists of krill. The third group contained a loose association of species which fed mainly on benthic organisms. *Notothenia gibberifrons* and *Notothenia squamifrons* are the important commercial species in this group.

Krill is the most important prey species to the fish in the South Georgia system during the austrial summer. It was consumed either directly or indirectly by all of the fish in this study. However, it is unknown whether the krill resource is limiting to these fish at that time or in any other season. More information on the seasonal dynamics and behavior of these fish and their prey is necessary to conclusively determine the role of competition for food in this system.

The potential for change in this community due to fishing is evident. Selective reduction in populations within the fish community may have widespread repercussions. The relatively simple, but highly interconnected, food web in the South Georgia system may have a lower potential for fish yield than previously thought (Hemple 1985).

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Abstract. – The school shark *Galeorhinus galeus* was sampled by otter trawl on the continental shelf of southern Brazil from 1980 to 1986 between latitudes 32°S and 34°40′S, at depths between 10 and 500 m. The species is a winter migrant, present in the study area from April to November. A total of 1548 specimens were examined. Sexual maturity occurred at total length of 107–117 cm in males, and 118–128 cm in females. The reproductive cycle was annual in the male and three years in the female, with uterine rest and slow vitellogenesis during the first year, maturation of oocytes and copulation during the second year, and gestation during the third year. In November, the diameter of mature follicle was 4.6–5.5 cm, ovulation occurred, and full-term embryos occurred with average total length of 30.3 cm. Uterine fecundity varied between 4 and 41 with a mean of 23.1, of which 94.2% were normal embryos, 5.2% were non-developing eggs, and 0.6% were abnormal embryos. Copulation took place up to 5 months before ovulation, with passive transport of spermatophores through the uterus. Liver weight as a percent of gutted body weight averaged 8% in immature animals of both sexes, 7% in gravid females, 11% in adult males and nongravid females in the first year of the reproductive cycle, and 17% in non-gravid females in the second year of the cycle, and it decreased during winter.

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Sexual Development, Reproductive Cycle, and Fecundity of the School Shark *Galeorhinus galeus* off Southern Brazil

Mônica Brick Peres
Carolus Maria Vooren

Fundação Universidade do Rio Grande, Depto. de Oceanografia
Caixa Postal 474, 96200 Rio Grande, RS, Brazil

Annual landings of demersal sharks at the port of Rio Grande, Brazil, increased from 1414 tons in 1973 to 3217 tons in 1986 and then decreased to 2023 tons in 1989 (SUDEPE 1990). This raises the question of the impact of increasing fishing effort on the stocks. The school shark *Galeorhinus galeus* comprises the major part of the landings (Wahrlich and Peres 1990). Accounts of fisheries for this species in other areas are classic examples of the rule that sharks are unable to maintain their abundance under heavy fishing. This is due to their live-bearing mode of reproduction, which implies that fecundity is low and recruitment is proportional to the abundance of the adults (Holden 1977). Management of the fishery requires estimates of reproductive parameters.

The reproductive cycle of female *G. galeus* has been described as annual off California and Tunisia, and biannual off Australia (Ripley 1946, Olsen 1984, Capapé and Mellinger 1988). However, the simultaneous occurrence of three distinct reproductive stages of adult females off southern Brazil led to the hypothesis of a triannual reproductive cycle (Vooren and Guzenski 1982). This hypothesis was tested in the present study.

This paper describes sexual maturation and the reproductive cycle for both sexes, and uterine and ovarian fecundity of female school shark off southern Brazil.

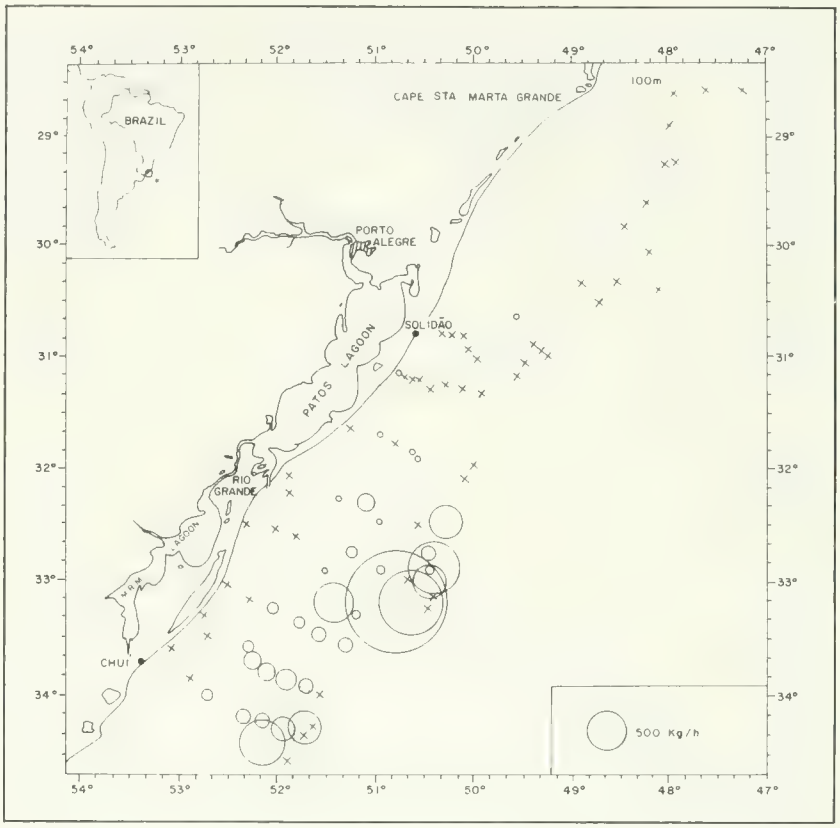
Materials and methods

The study area was the continental shelf of Rio Grande do Sul, between Cape Santa Marta Grande (lat. 28°40′S) and Chuí (lat. 33°44′S), Brazil. From June 1980 to September 1986, the area was surveyed during 12 cruises by the RV *Atlântico Sul*, at depths between 10 and 500 m, using an otter trawl with groundrope of 50 m and codend mesh of 45 mm between opposed knots (see Fig. 1 for location of stations). Tows lasted 60 minutes, and towing speed was 5.5 km/hour. Samples were also obtained with similar nets during five commercial trawling trips. The data series includes all months of the year except December and March. One specimen found on 13 December 1985 on the beach near Rio Grande, and nine specimens obtained on 24 June 1986 from commercial landings at Montevideo, were also examined.

In each haul, the weight of the catch (in g) and the body length (in cm) and sex of all specimens were recorded. Total length (TL) was measured with the tail aligned with the long axis of the body. Biological data were taken from random samples of the catches, totaling 904 females of 43.0–154.5 cm TL and 644 males of 43.5–148.0 cm TL. Weights (in g) of the whole body, liver, and gonads were recorded. Total body weight was measured until November 1983. Thereafter, the eviscerated body

Figure 1

The study area with sampling grid for the school shark *Galeorhinus galeus*, during 9–30 August 1983 (depths <100 m) and 17 July–17 September 1986 (depths of 100–500 m) off Brazil. Surface area of circles indicates catch rates in kg/hour bottom trawling, and crosses indicate zero catches.



weight was measured, as recommended by Mellinger (1966), for study of certain aspects of reproduction. The gonad weight included that of the epigonal organ cut in front of the rectal gland. Epigonal organ weights were also measured in 43 specimens. In males, the length of the clasper was measured from the posterior origin of the pelvic fin. For females, the following data were recorded: diameter and color of the largest ovarian follicle, width of the nidamentary gland, presence or absence of embryos and uterine eggs, weight of the full gravid uterus, and greatest width of the nongravid uterus. Embryos were measured, sexed, and weighed with and without the yolksac. Fecundity was determined by counting maturing ovarian follicles ("ovarian fecundity") and uterine eggs and embryos ("uterine fecundity"). Hepatosomatic and gonadosomatic indices were calculated, using the weight of the organs as a percent of the eviscerated body weight. The latter indices were obtained using the linear regression equation of eviscerated weight as a function of total length. Separate equations were used for sexually immature sharks of both sexes, adult males, and adult females (Table 1).

Histological smears of the reproductive organs were obtained from 7 males and 17 females, ranging from 124 to 148 cm TL. Testes smears were made from cross-section surfaces on glass slides. The nidamentary gland was opened lengthwise and smears were made of the surface of its lumen on glass slides. Smears were also made of the contents of the epididymis and the seminal vesicle. Smears were fixed in a solution of equal proportions of ethanol and ethyl ether and stained with haematoxylin-eosin.

The present study follows Compagno (1988) with respect to nomenclature.

Table 1

Biometric variables (Y) as a function of total body length (TL) in *Galeorhinus galeus* from Rio Grande do Sul, Brazil. TL* indicates body length of the mother, *N* indicates sample size, *R* is correlation coefficient. Weights in g, lengths in cm.

Variable	Equation	*N*	*R*
Eviscerated weight, adult male	$Y = 3.95 \times 10^{-3} \times TL^{2.95}$	124	0.91
Eviscerated weight, adult female	$Y = 5.38 \times 10^{-4} \times TL^{3.39}$	128	0.93
Eviscerated weight, immatures	$Y = 2.15 \times 10^{-3} \times TL^{3.10}$	138	0.99
Weight of testis	$Y = -5.20 TL^{3.32}$	131	0.74
Weight of epigonal organ, male	$Y = -4.67 TL^{2.89}$	13	0.94
Ovarian fecundity	$Y = 0.49TL - 43.15$	57	0.68
Uterine fecundity	$Y = 0.53TL - 49.44$	137	0.66
Mean length of embryo per litter, June–July	$Y = 0.025TL^* + 18.78$	39	0.13
Mean length of embryo per litter, Aug–Sep	$Y = 0.14TL^* + 7.24$	46	0.44

Results

Spatial and temporal distribution

School sharks were seasonally abundant at depths of 40–350 m, between latitudes 32°S and 34°30′S. In this area, mean catch rates per cruise were high from June to September, attaining values up to 376 kg/hour at depths between 40 and 100 m, and 620 kg/hour between 100 and 350 m. Figure 1 shows the sampling grid and catches for August 1983 and 17 July–17 September 1986. Within the study area, the entire area of distribution was covered by the sampling grid.

The species was scarce in April, May, October, and November, and absent in January and February. The school shark is characterized as a seasonal migrant, entering the study area in autumn, attaining peak abundance during winter, and leaving in spring.

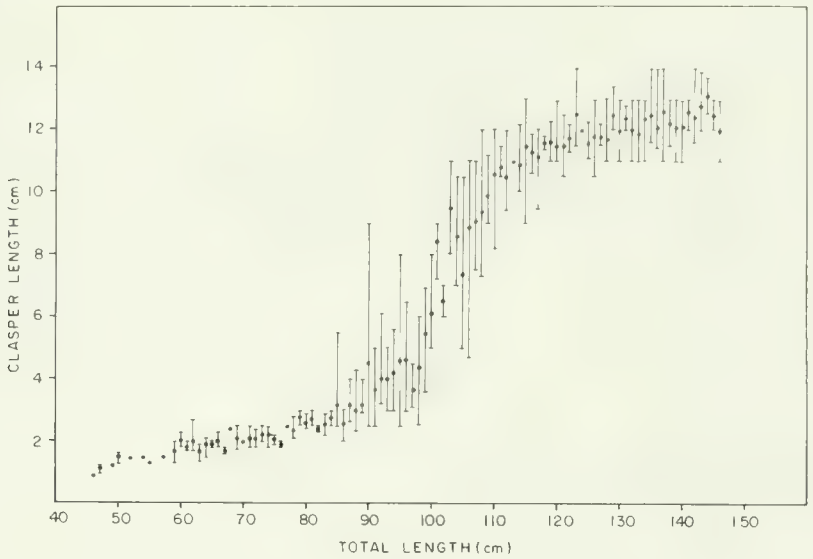


Figure 2

Relationship between total body length and length of clasper in the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil. Points indicate the mean, and vertical lines the range for length-class intervals of 1 cm.

Sexual development and organization of gametes in the male

Sexual maturation of the male was inferred from the length of the clasper. The relationship between clasper length and total length was sigmoid (Fig. 2). The curve rose steeply between 85 and 117 cm TL, and dispersion was greatest in this range. The curve flattened out for clasper lengths greater than 10.5 cm. This latter value was taken as the lower limit for sexual maturity. On the basis of this criterion, sexual maturation began at 85 cm TL. The smallest mature male measured was 107 cm TL, 50% maturity occurred at 111 cm, and all males greater than 117 cm were mature. The clasper of the adult measured, on average, 12.0 cm, ranging from 10.5 to 14.0 cm.

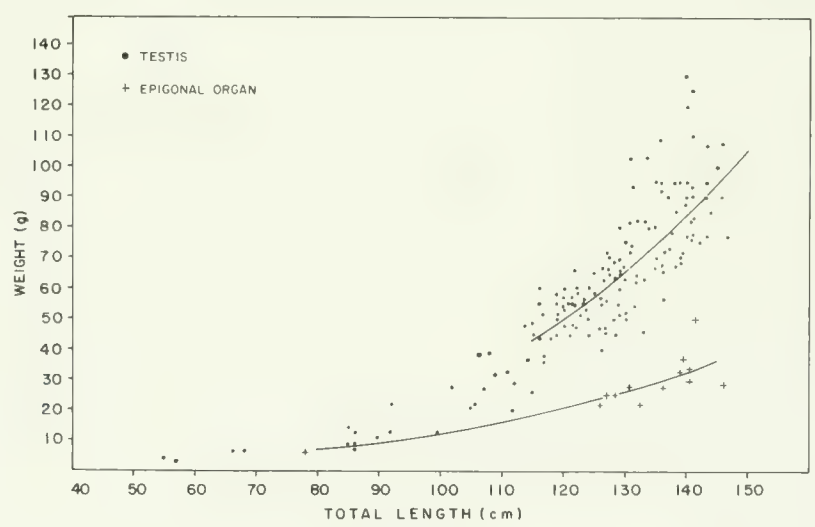


Figure 3

Relationship between total body length and weight of epigonal organs and testis in the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

Potential equations described adequately the relationship of gonad and epigonal organ weight to total length (Fig. 3, Table 1). At total lengths less than 85 cm, gonad weight was similar to the weight of the epigonal organ, and testes were not visually evident. Between 85 and 140 cm TL, epigonal organ increased from 10 to 30 g, and gonad weight increased to an

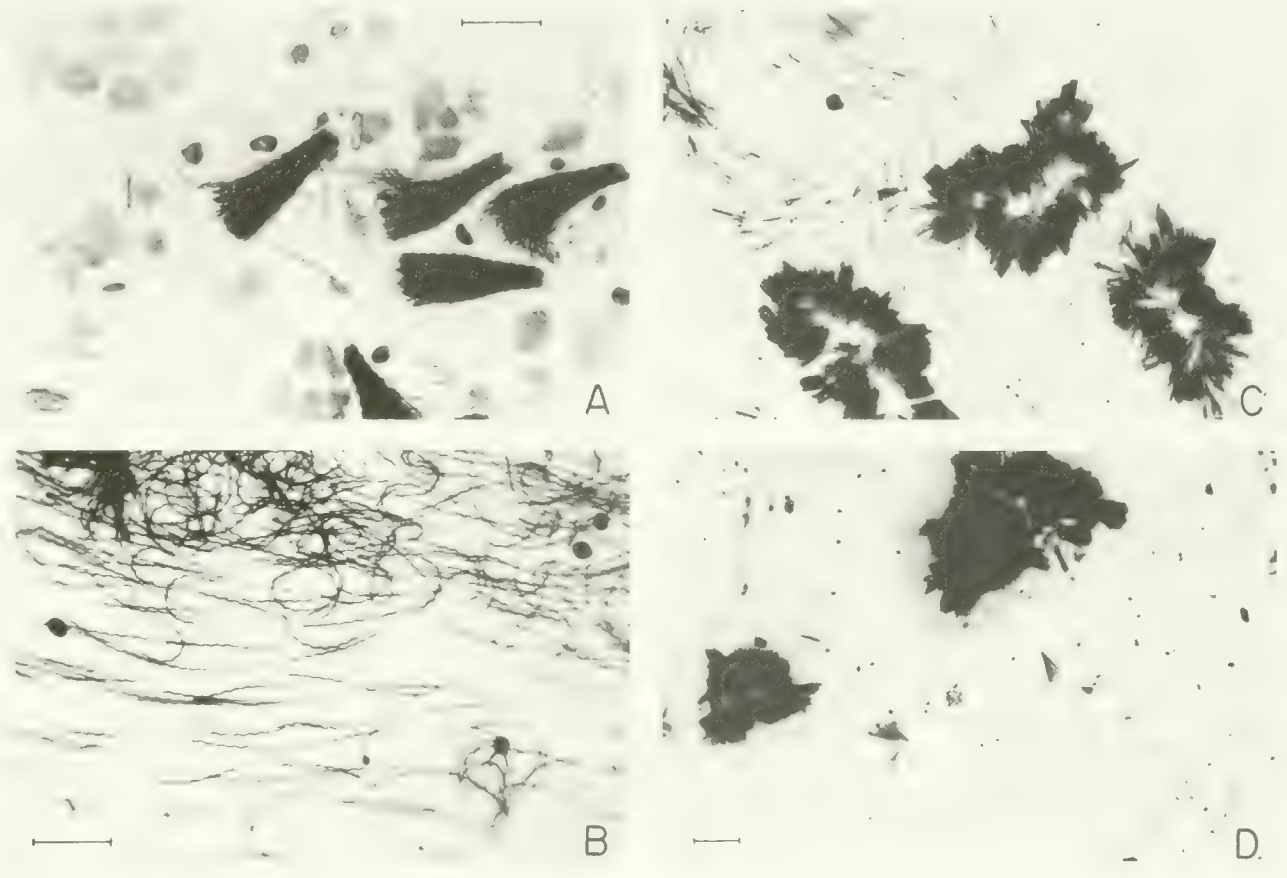


Figure 4

Spermatozoa in smears of reproductive organs of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil. (A) testis, (B) epididymis, (C) seminal vesicle, (D) nidamentary gland of an adult nongravid female with mature ovary. Scale bars represent 20 μm.

average of 90 g. Thus, the increase of gonad weight with body size reflects mostly growth of the testes, and can be interpreted in terms of sexual development. The gonadosomatic index varied about the mean of 0.6 at total lengths less than 117 cm, and 0.9 at greater body lengths. The attainment of sexual maturity, as indicated by the clasper, was accompanied by a marked increase in relative weight of the testes. Growth of the testes continued after the attainment of sexual maturity, as indicated by gonad weights of 35–60 g at 115 cm TL, and 75–130 g at 145 cm TL.

Smears of the testes showed that sperm occurred in bundles within the testicular ampullae (Fig. 4A). In the epididymis, sperm occurred singly (Fig. 4B). The head of the spermatozoon measured, on average, 47 μm and the tail about 100 μm (n 62). In all smears of the seminal vesicle, sperm occurred in circular or oblong agglomerations, with their heads towards the center (Fig. 4C). Such structures were called spermatophores. The shortest and longest axes of the spermatophores measured, on average, 142 and 201 μm, respectively (n 64).

Sexual development of the female

The female has one functional ovary, situated on the right. Ovarian follicles were visible to the naked eye at total lengths greater than 80 cm. Follicle color varied with its diameter: transparent and colorless, up to 0.6 cm; opaque white, 0.4–1.2 cm; pale to sulphur yellow, 1.0–2.5 cm; and golden yellow, 3.5–5.5 cm. Follicles of ovulating females ranged from 4.6 to 5.5 cm, which is therefore the size range of the mature follicle. The weight of 58 mature ovaries increased with body size

and varied from 400 to 1600g, including the epigonal organ of 25–60g. Maturing ovaries contained 12 to 34 follicles of uniform size, with diameter greater than 3.5cm. Such ovaries occurred in females larger than 122cm TL (Fig. 5).

The smallest pregnant female was 118cm TL. Incidence of pregnancy increased to about 50% at body sizes greater than 130cm (Table 2). The developing uterus appeared as a strip of white tissue with diameters up to 0.3cm in females of less than 110cm. The uterus widened first at its posterior end, becoming bottle-shaped at lengths of 110–125cm TL, with a diameter of 1.0–2.3cm at its widest part. Fully-formed uteri, uniform in width, measured 2.0–4.0cm in diameter and occurred in females larger than 121cm TL. All nongravid females with total lengths greater than 128cm possessed such uteri.

The width of the nidamentary gland varied about 0.4cm in females of less than 112cm, and increased to values between 1.8 and 4.6cm in females larger than 125cm TL (Fig. 6).

Based on color and size of the ovarian follicle, width of the nidamentary gland and uterus, and the incidence of pregnancy, it is concluded that sexual maturity first occurred at 118cm TL, 50% maturity at 123cm TL, and full maturity at 128 cm TL. In the nongravid adult female, the uterus had a diameter of 2.0–4.0cm, the nidamentary gland was 1.8–3.5cm in width, and the ovary contained yellow follicles of diameters 1.4–5.5cm.

In one nongravid female of 154.5cm TL, the ovary was reduced to four atretic follicles with diameters less than 0.4cm, and the nidamentary glands were reduced in width (Fig. 6). The dorsal coloration of the body of this female was light grey with dark blotches. This 41-year-old female (Ferreira and Vooren 1991) was considered senile, the only such specimen encountered.

Reproductive cycle of the female

If the reproductive cycle of the female is synchronous at the population level, fertilization and birth should occur at definite seasons, and at any given time all gravid females should contain embryos in the same stage of development. If, in addition, the reproductive cycle lasts three years, three distinct categories of adult females are expected to simultaneously exist. A time-series of measurements of embryos and ovarian follicles, histological smears of the nidamentary gland, and seasonal records of ovulation showed that this was the case.

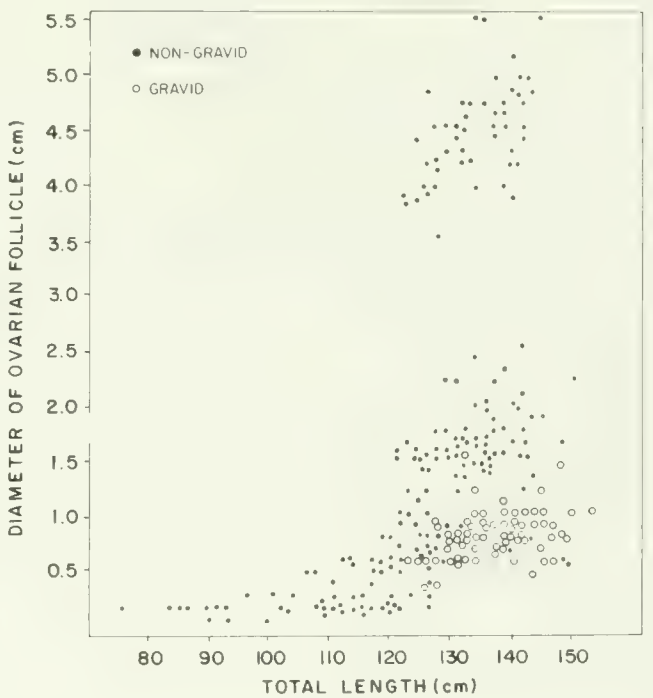


Figure 5

Relationship between total body length and diameter of the largest follicle in the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

Table 2

Incidence of pregnancy in *Galeorhinus galeus* from Rio Grande do Sul, Brazil, as a percent of the sample (n), by classes of total length (TL) in cm.

TL	% pregnant	n	TL	% pregnant	n
115	0	5	135	52	21
116	0	3	136	50	14
117	0	7	137	50	16
118	13	8	138	46	22
119	0	8	139	73	26
120	11	9	140	75	16
121	0	7	141	62	21
122	0	9	142	50	18
123	13	16	143	50	14
124	10	10	144	57	14
125	36	11	145	75	8
126	14	22	146	100	8
127	32	19	147	100	3
128	42	19	148	67	3
129	30	20	149	71	7
130	42	12	150	0	1
131	56	25	151	100	2
132	50	12	152	100	1
133	38	16	153	0	2
134	62	21	154	50	2

Within the study area, gravid females occurred from April to December and nongravid adult females from June to November. Ovulating females, females which had recently commpleted ovulation, and the largest mature ovarian follicles occurred in November and December. Full-term embryos without the yolksac were observed in November, as was also noted by De Buen (1952) off Uruguay. The monthly-length frequency distributions of embryos were unimodal, and modal embryonic total length increased from 13cm in April to 31cm in November (Fig. 7). Ovulation and birth both occurred in November–December, therefore gestation lasts 12 months.

In gravid females (GR), ovarian follicles were opaque white and did not grow (Fig. 8). Two distinct types of nongravid females occurred during the same time-periods each year. First-year nongravid females (NGR-1) occurred from June to September and had light-yellow ovarian follicles 0.5–2.5cm in diameter. Second-year nongravid females (NGR-2) were present July to November and had golden-yellow follicles of 3.5–5.5cm diameter.

From June to September, follicle diameter of NGR-1 females remained about 1.5cm (Fig. 9), while ovary weights ranged from 70 to 130g. Thus, vitellogenesis was slow. Females over the full size range of adults were classified as NGR-1 (Fig. 5). This category included the maturing, virgin phase but consisted mainly of resting females.

In NGR-2 females, the modal diameter of the largest follicle increased from 4.2cm in July to 5.5cm in November (Fig. 9). Accelerated vitellogenesis and ovarian maturation occurred in this phase. In November, these females had dilated nidamentary glands (the four greatest values in Fig. 6) and uteri containing a transparent viscous material resembling egg white.

The reproductive cycle of the female lasts three years. During the first 12 months after parturition, the oviduct remains in a resting stage and vitellogenesis is slow (NGR-1 stage). During the following 12 months, large mature follicles are produced, and the nidamentary gland and uteri are prepared for ovulation, which occurs in November–December (NGR-2 stage). Gestation lasts 12 months, during which there is no vitellogenesis, and parturition takes place in November–December (GR stage).

Nidamentary gland smears from one of eight NGR-2 females, collected in July 1986, had a large number of whole spermatophores, similar to those observed in the seminal vesicle of the male (Fig. 4). Thus, mating apparently begins during the NGR-2 phase as early as July, at least five months before ovulation, and the sperm is carried to the nidamentary gland by passive transport.

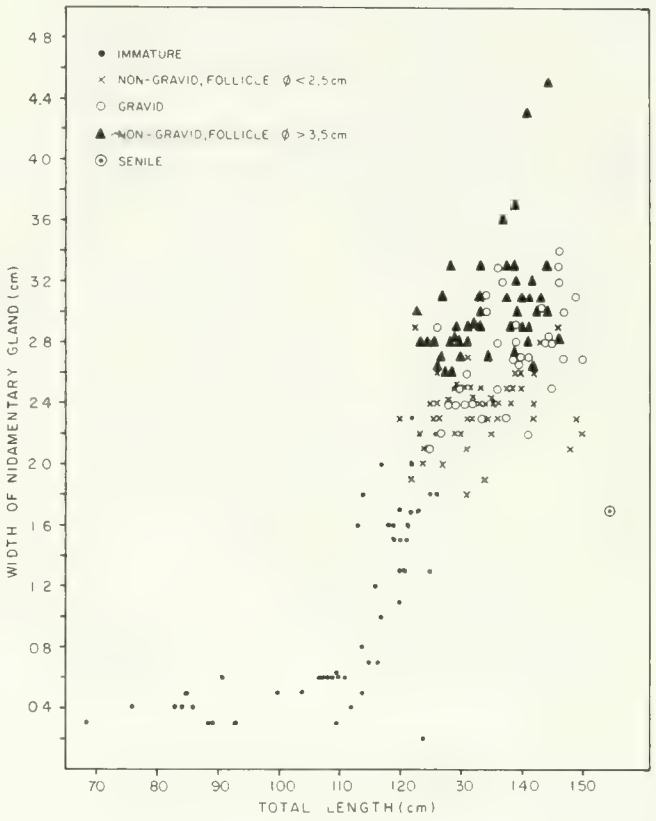


Figure 6
Relationship between total body length and width of the nidamentary gland in the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

Fecundity

Fecundity increased linearly with body size of the female (Table 1, Fig. 10). In 58 NGR-2 females of 123–146cm TL, ovarian fecundity ranged from 12 to 34 with a mean of 22.7 per female. In 140 females of 123–154cm TL, uterine fecundity ranged from 4 to 41 with a mean of 23.1. Of the items in the uteri, 94.2% were normal embryos, 5.2% were nondeveloping eggs, and 0.6% were dead or abnormal embryos. In 79% of the gravid females, there were at least one or two nondeveloping eggs, but the total number of these eggs per female, ranged up to 34.

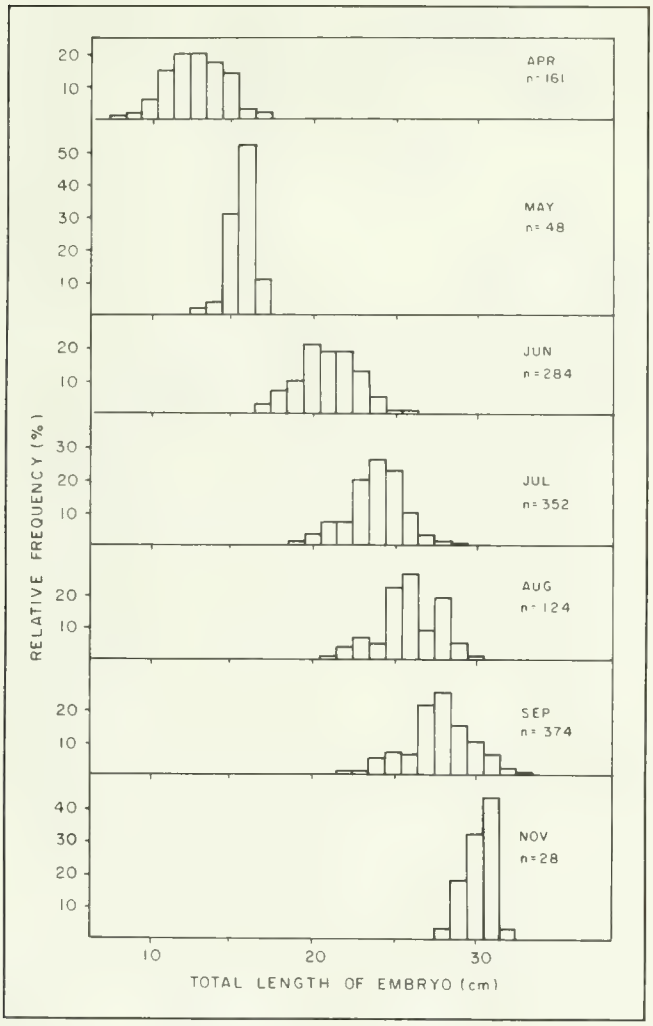


Figure 7 (above)
Monthly distributions of relative frequencies of total length of embryos of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

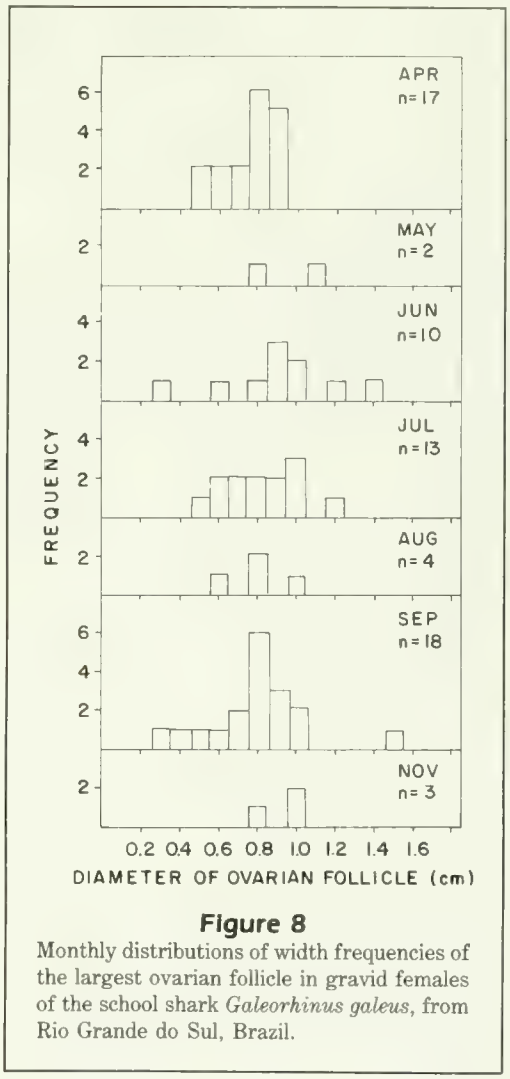


Figure 8
Monthly distributions of width frequencies of the largest ovarian follicle in gravid females of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

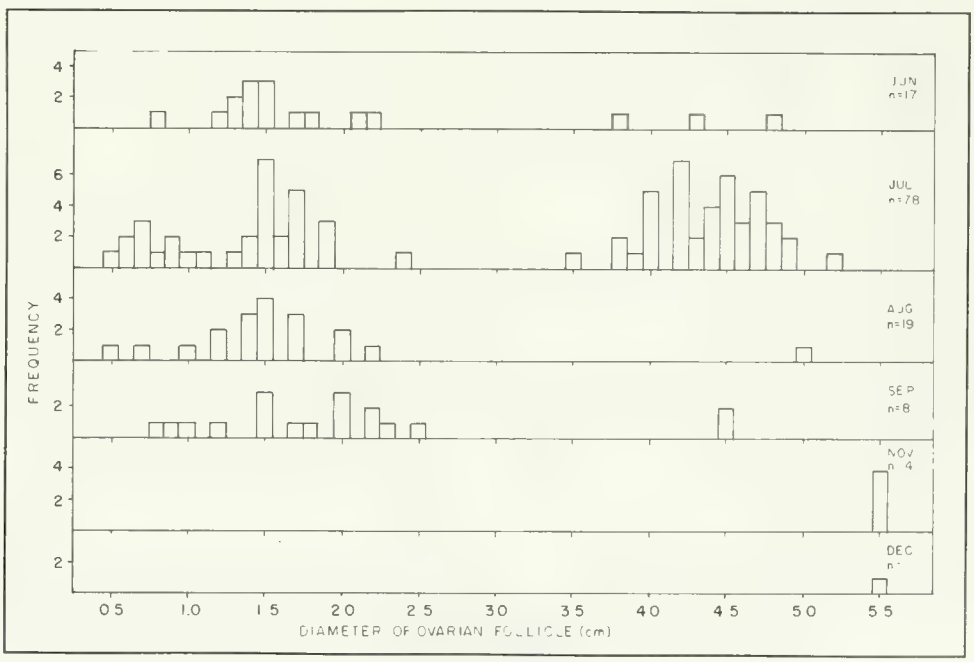


Figure 9 (right)
Monthly distributions of width frequencies of the largest ovarian follicle in nongravid adult females of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

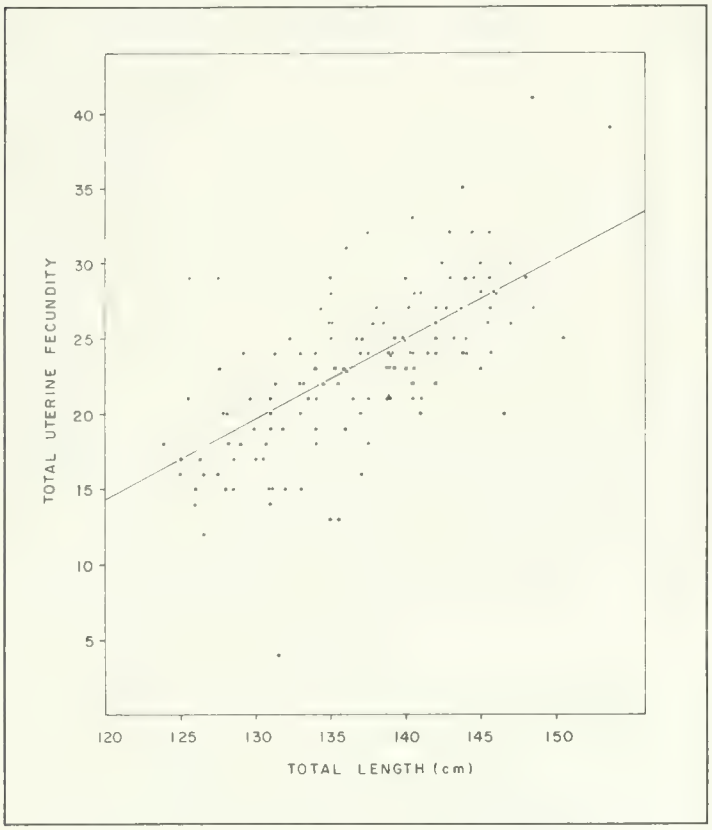


Figure 10
Relationship between total body length and uterine fecundity in the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

Gestation

Outgrowths of the uterine wall divided the uterus into separate gestation chambers for each embryo. The quantity of liquid in the chambers of the two uteri increased from about 200 g in April to 500–900 g in July, constituting respectively 8.3 and 28.0% of the weight of the full uteri in those months. Uteri were swollen and turgid due to the increasing mass of the litter and liquid, and in July attained weights between 1230 and 5520 g.

Embryos situated near the cloaca were about 2–4 cm larger than those situated near the nidamentary gland. In August and September, but not in April, mean total length per litter increased linearly with total length of the mother (Table 1, Fig. 11). This indicates that embryos grow faster in the larger females.

The weight of 38 large follicles of ovulating females varied from 42 to 56 g. The weight of 59 newly ovulated eggs varied between 40 and 100 g with a mean of 59.4 g, which is the magnitude of the yolk reserve in the egg. From April to September, mean total length and yolkless weight of the embryos increased from 13.3 to 28.0 cm and from 10.0 to 65.0 g, while the weight of the full yolksac decreased from 45 to 17 g. There was no yolksac in a litter of 28 embryos in November. These embryos averaged 30.3 cm TL and 92.9 g total weight. The sex ratio of embryos did not differ significantly from unity: 599 were males and 625 were females.

Cycle of the liver

In sexually immature sharks, the hepatosomatic index (HSI) did not change with body size but varied about the mean of 7.9 throughout the range of total lengths. The HSI of males increased at sexual maturity to a mean of 11.4 (Fig. 12).

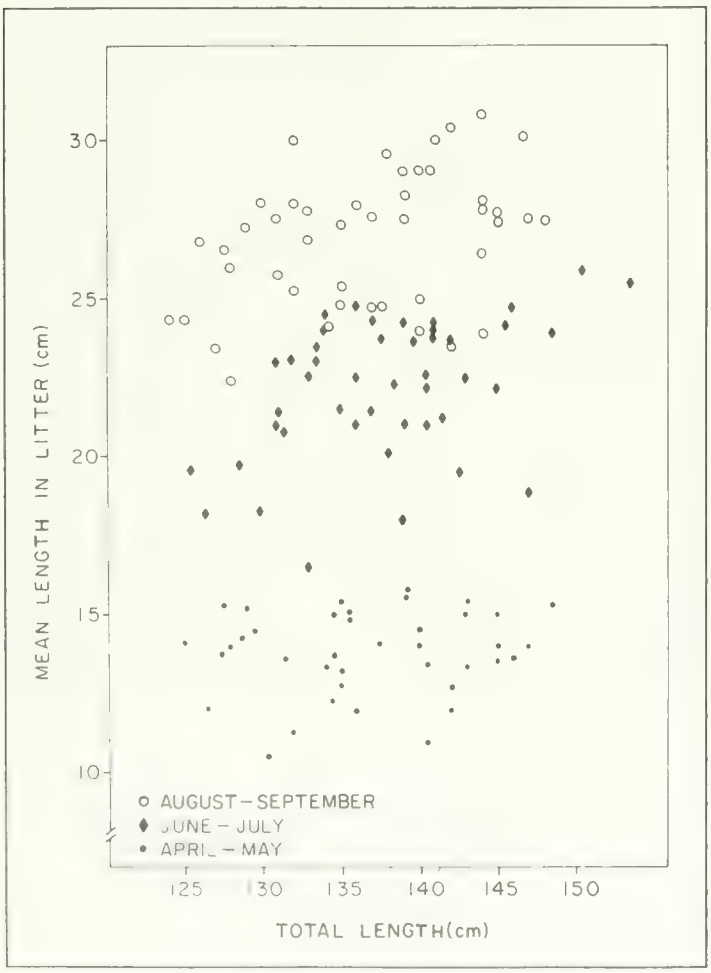


Figure 11
Relationship between total body length of the mother and mean length in litter of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

The HSI of adult females varied during the reproductive cycle; the mean was 7.2 in GR females, 10.8 in NGR-1, and 17.2 in NGR-2 females (Fig. 13). In all categories, the mean monthly HSI decreased from a maximum in early winter to a minimum in spring (Fig. 14).

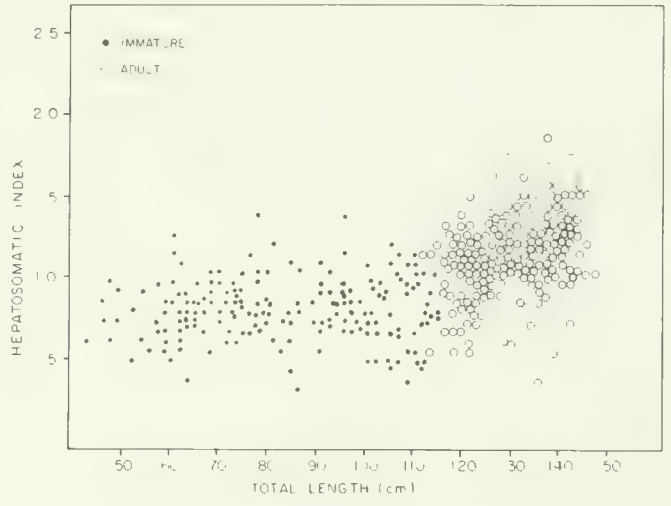


Figure 12

Relationship between total body length and hepatosomatic index of males of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil.

Discussion

Body size at attainment of sexual maturity, as a percent of maximum size, and the slope of the linear regression of fecundity on total length are similar in the western South Atlantic, Australian, and eastern North Pacific populations of the school shark (Table 3, Fig. 15). It is concluded that these parameters of reproduction are characters at the species level.

The dense groups of spermatozoa in the seminal vesicles of adult males of the school shark were designated spermatophores, in analogy with structures described in the basking shark *Cetorhinus maximus* and the blue shark *Prionace glauca* (Matthews 1950, Pratt 1979). During the present study, spermatophores were also found in the seminal vesicle of the smooth dogfish *Mustelus canis* and the sand shark *Eugomphodus taurus*. It seems that the grouping of spermatozoa in dense agglomerations is a commom feature in elasmobranchs.

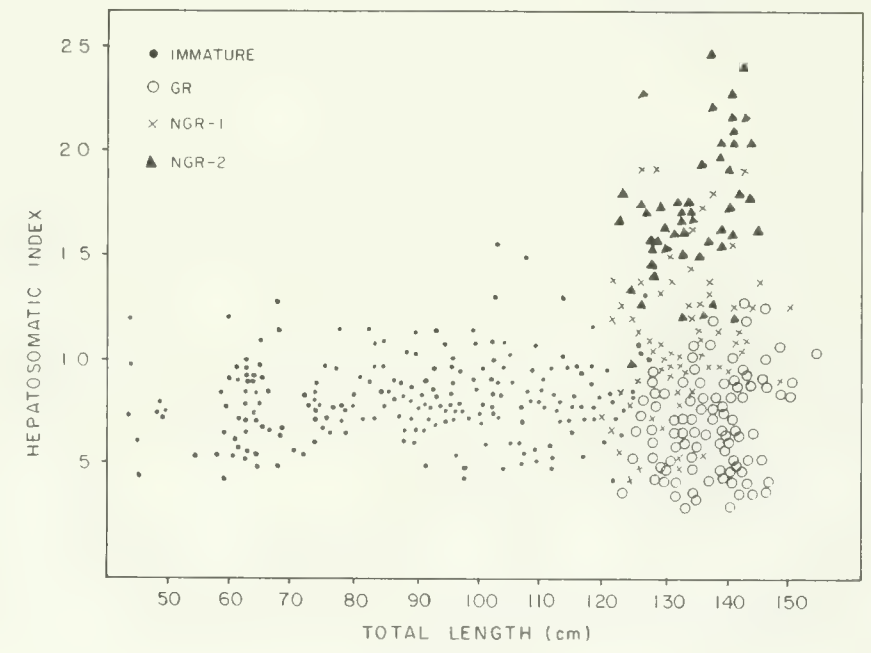


Figure 13

Relationship between total body length and hepatosomatic index of females of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil, in different stages of the reproductive cycle. GR, gravid; NGR-1, 1st year nongravid; NGR-2, 2d year nongravid.

There is no discontinuity in the gonadosomatic index of school shark adult males, such as would indicate the simultaneous existence of different reproductive stages, as was observed in females. All smears of the seminal vesicle of adult males in July contained spermatophores. It is concluded that all adult males present in the area during winter are in the mating stage.

In the western South Atlantic population, copulation occurs up to at least 5 months before ovulation. Gestation is highly synchronized, with all phases from ovulation to birth being timed at the population level. This requires that at a particular period each year, all NGR-2 females will have mated and will be ready to ovulate. The extended mating period ensures this. The same is observed in the blue shark, where the female mates up to 12 months before ovulation (Pratt 1979).

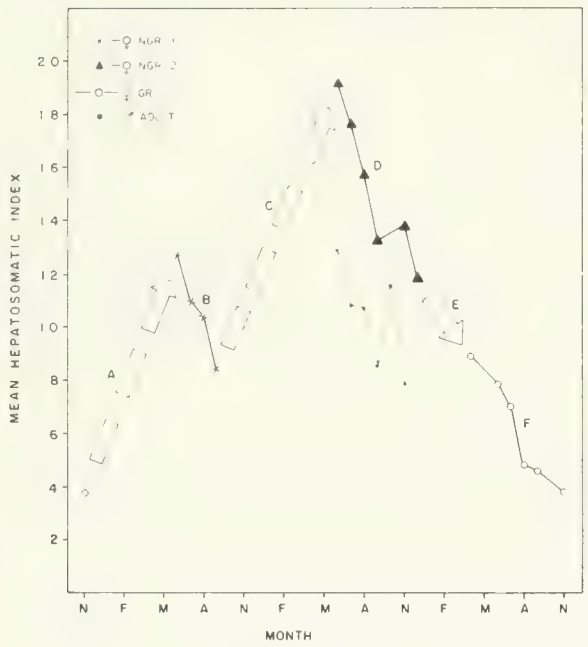


Figure 14

Mean monthly hepasomatic index of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil, in different reproductive stages. GR, gravid; NGR-1, 1st year nongravid; NGR-2, 2d year nongravid.

Table 3

Total length (TL, in cm) and age (years) at stages of sexual development in geographical populations of *Galeorhinus galeus*. Data on the Australian population after Olsen (1984) and on the eastern North Pacific population after Ripley (1946). Age in the western South Atlantic population after growth curve by Ferreira and Vooren (1991). Length ratio expresses TL at first maturity, as a percent of observed maximum values.

	SW Atlantic	Australia	NE Pacific
Male			
TL 1st maturity	107.0	120	135
Age 1st maturity	10.5	8	—
TL 50% maturity	111.0	—	142
Age 50% maturity	11.4	—	—
TL full maturity	117.0	132	175
Age full maturity	13.2	10	—
TL maximum	148.0	155	185
Age maximum	36.1	41	—
Length ratio	72.3	77.4	73.0
Female			
TL 1st maturity	118.0	135	150
Age 1st maturity	14.1	12	—
TL 50% maturity	123.0	—	158
Age 50% maturity	15.7	—	—
TL full maturity	128.0	—	180
Age full maturity	17.5	—	—
TL maximum	154.5	174	195
Age maximum	36.2	53	—
Length ratio	76.1	77.6	76.9

Ripley (1946) concluded that in eastern North Pacific animals, gestation lasts 12 months during which there is no vitellogenesis and that parturition occurs in summer. Data on the female cycle in this population were obtained from a single sampling area where, in a sample of 3747 females, 88% were gravid, 11% had large ovarian follicles, and 1% were resting. The percentages reflect the situation at a certain point of the migration route of the gravid females, but the data indicate the simultaneous presence of three categories of adult females. In winter, Olsen (1954) observed two types of nongravid Australian females: one with the largest ovarian follicles ranging from 4.0 to 5.0 cm in diameter, and the other with maximum follicle diameters of 1.0–2.0 cm. These two categories occurred simultaneously and in similar numbers. Parturition took place in November–December, and size at birth was about 31 cm TL. Olsen (1954) assumed that gestation starts immediately after mating in winter and lasts 6 months. The presence of the two nongravid categories was explained by a period of 18 months for the production of the mature follicle, giving a cycle of 2 years. However, in view of the data on gestation in western South Atlantic and eastern North Pacific animals, it is unlikely that this phase lasts only 6 months in Australian animals. Therefore, we conclude that the duration and timing of the reproductive cycle are similar in these three populations of school shark.

The observed increase in body size of embryos from the anterior to the posterior end of the uterus has also been noted in eastern North Pacific and Australian animals. This may partly reflect duration of the ovulation process, during which eggs enter the oviducts in pairs at intervals of 24–48 hours in the smooth dogfish, in the skates, *Raja brachyura* and *Raja erinacea*, and in the sand shark (TeWinkel 1950, Holden 1974, Gilmore et al. 1983). Assuming an interval of 36 hours in the school shark, the duration of ovulation for all eggs would range between 10 and 40 days, depending on fecundity. The size difference between the first and the last embryo in the uterus would then reflect the growth of the first embryo during the ovulation period, although the possibility of a corresponding difference in yolk reserve remains to be investigated.

In spring, liver weight as a proportion of total body weight (HSI) of the eastern North Pacific adult female NGR-2 was 14%, and about 4% in GR females. In the

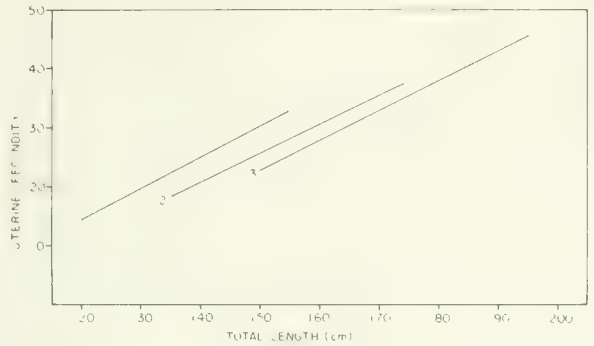


Figure 15

Relationship between total body length and uterine fecundity of the school shark *Galeorhinus galeus*, of (1) southern Brazil; (2) southern Australia, according to Olsen (1984); and (3) California, according to Ripley (1946).

Australian animals, the HSI ranged from 6.0 to 11.0 in GR females, and from 15.0 to 24.0 in NGR-2 females (Olsen 1954). Since these values are similar to those of comparable eastern South Atlantic females, it is concluded that the liver cycle of adult females observed in the present study is characteristic of the species.

When estrogen was administered to the female of the spotted catfish *Scyliorhinus canicula*, the liver increased in size and produced vitellogenin and released it into the blood (Craik 1978). Estrogen is produced by the granulosa of the maturing ovarian follicle of the spiny dogfish *Squalus acanthias*, and by the mature testis of *Torpedo marmorata*, *Scyliorhinus canicula*, *Squalus acanthias*, and *Raja clavata* (Lance and Callard 1969, Craik 1978, Dodd 1983). This explains why in the western South Atlantic school shark the HSI increases in both sexes after sexual maturation and varies with the cycle of the adult ovary, reaching a maximum during the NGR-2 stage. Ripley and Bolomey (1946) show that in spring the proportion of oil in the liver of the eastern North Pacific adult is about 60% in males and NGR-1 females, 40% in GR and postpartum females, and 70% in NGR-2 females and those with uterine eggs. Thus, the changes in HSI of the adult female reflect a major variation in the quantity of lipids in the liver during the reproductive cycle.

The submerged weight (SW_i) in seawater of an object i can be determined by the model

$$SW_i = m_i (1 - d_s / d_i),$$

where m_i is the mass of the object in g, and d_s and d_i are the specific densities of seawater and of the object, respectively, in g/cm^3. A negative submerged weight indicates buoyancy. Using this model, submerged weight for the eviscerated body and the oil reserve in the liver was calculated for males and females of 130 cm TL in all three reproductive stages. For submerged weight of the body, m_i was calculated from the regressions in Table 1, and d_i was estimated at 1.065 g/cm^3, which is the mean of the liver-free body density of 13 species of sharks (Baldridge 1970). For submerged weight of the oil reserve, the liver mass calculated from the HSI in the present study was multiplied by the percentage of oil in the liver in the eastern North Pacific school shark. For the specific density of the liver oil in the different reproductive stages, values from Bone and Marshal (1982) were used: GR females, non-metabolizable lipids, 0.860 g/cm^3; NGR-2 females, metabolizable lipids, 0.930 g/cm^3; NGR-1 and males, the median of these values, 0.895 g/cm^3. To calculate the submerged weights of the mature ovaries of NGR-2 females 130 cm TL, the regression of ovarian fecundity on total length was combined with data on mass and volume of 14 follicles (4.0 cm in diameter).This resulted in an ovary mass of 665.00 g and a specific density of 1.108 g/cm^3. The specific density of seawater was taken as 1.024 g/cm^3, according to Baldridge (1970).

The results are summarized in Table 4. In males and NGR-1 females, the buoyancy of the liver is about one-fourth the submerged weight of the eviscerated body. In NGR-2 females, the increased liver buoyancy compensates for 60% of the submerged weight of the yolk mass in the ovary. Through the production of estrogen, the maturing ovary also controls, simultaneously, the vitellogenic and hydrostatic functions of the liver. Besides providing buoyancy when this is most needed, the metabolic reserve of the NGR-2 female guarantees resources for vitellogenesis and maturation of the follicle, thus ensuring the timing of reproduction.

The specific density of embryos, for example, 1.035 g/cm^3 in the sandbar shark *Carcharinus milberti* (Baldridge 1970), is much less than that of yolk. During gestation of aplacentary sharks, some organic matter in the yolk reserve is lost but water is absorbed, and the full-term embryo weighs twice as much as the yolk (Ranzi 1932). The specific density of the uterus decreases during gestation because of the increase of intrauterine liquid and embryos and the decrease of egg yolk. This enables the gestating female to metabolize her lipid reserves without loss of buoyancy, and explains the low liver buoyancy in this stage. The reduction in liver volume also provides space for the gravid uteri. Such a trade-off between lipids and water without change in overall buoyancy also occurs during the winter fasting of *Clupea harengus* (Iles 1984).

Table 4

Submerged weight of parts of the body in *Galeorhinus galeus* from Rio Grande do Sul, Brazil. NGR-1, 1st year nongravid; NGR-2, 2d year nongravid; GR, gravid.

Item	Submerged weight (g)
Adult male, liver oil	−73.9
NGR-1 female, liver oil	−71.9
NGR-2 female, liver oil	−100.4
GR female, liver oil	−42.3
Adult male, eviscerated body	+288.7
Adult female, eviscerated body	+296.4
NGR-2 female, mature ovary	+50.4

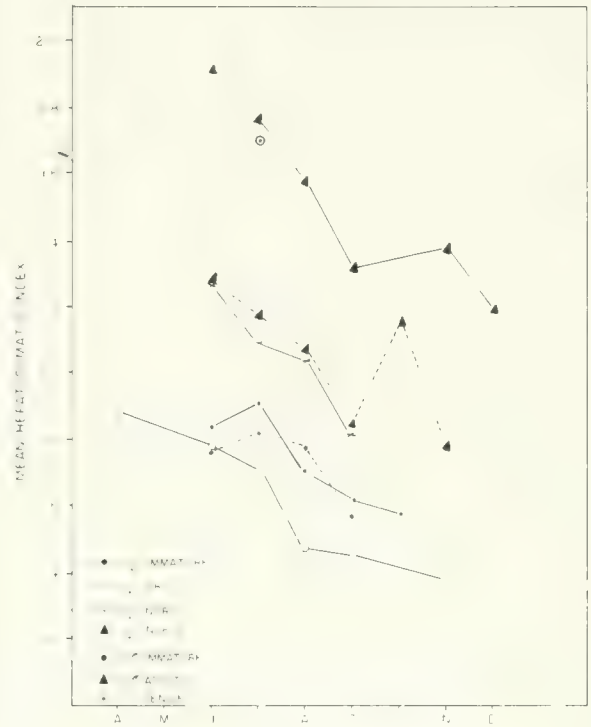


Figure 16

Mean monthly hepatosomatic index during the reproductive cycle of the school shark *Galeorhinus galeus*, from Rio Grande do Sul, Brazil. NGR-1, 1st year nongravid; NGR-2, 2d year nongravid; GR, gravid. Arrows indicate the hypothetical pattern during periods when the population occurs outside the study area.

The gradual decrease of the HSI in both sexes during winter suggests that at that time, the population invests little effort in feeding and lives mostly off its lipid reserves. From interpolation in the observed HSI pattern, it is concluded that during the first two summers after parturition, the female accumulates lipids. During the third year of the cycle, HSI decreases constantly from ovulation to parturition (Fig. 16). In coastal waters of Uruguay, the species is caught by bottom gillnets during winter and by bottom longlines during summer (De Buen 1952). This is consistent with the hypothesis of the endogenous periodicity of feeding under hormonal control, as in *Clupea harengus* (Iles 1984). It is suggested that in the school shark, feeding during winter is reduced to the intake of proteins necessary for the continuous production of urea. In the liver of the female, a seasonal and a three-year cycle are timed to store and metabolize lipid reserves, to synthesize and transfer vitellogenin, and to control buoyancy, in a sequence which corresponds with the varying physiological needs during the reproductive cycle.

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Differential Selection of Crab *Chionoecetes opilio* and *Hyas* spp. as Prey by Sympatric Cod *Gadus morhua* and thorny skate *Raja radiata*

David A. Robichaud

Department of Fisheries and Oceans, Biological Station
St. Andrews, New Brunswick, E0G 2X0 Canada

Robert W. Elner

Department of Fisheries and Oceans, Biological Station
St. Andrews, New Brunswick, E0G 2X0 Canada
Present address: Canadian Wildlife Service
Box 340, Delta, British Columbia B4K 3Y3 Canada

Richard F.J. Bailey

Department of Fisheries and Oceans, Biological Station
St. Andrews, New Brunswick, E0G 2X0 Canada
Present address: Department of Fisheries and Oceans, Institut Maurice-Lamontagne
P.O. Box 1000, Mont-Joli, Quebec, G5H 3Z4 Canada

Abstract. – During 1981 and 1982, 933 Atlantic cod *Gadus morhua* and 119 thorny skate *Raja radiata* were collected off the northwestern coast of Cape Breton Island, Nova Scotia. Danish seines, jigs, gillnets, and trawls were used for sampling. Stomach contents were analyzed to investigate predator-prey relationships between cod and snow crab *Chionoecetes opilio*, two commercially important species. For comparison, skate and two toad crab species, *Hyas araneus* and *H. coarctatus*, were also considered.

During spring (April, May), cod fed mostly (by weight) on large soft-shelled male snow crab [77–110 mm carapace width (CW)]. In summer (July) and fall (September), cod predation was directed more towards prey species such as fish, although the mean number of snow crab per cod stomach also increased. The average number of snow crab in cod stomach contents was higher (0.59 crab/stomach) on sand and mud bottoms than on rocky and gravel bottoms (0.05 crab/stomach). In contrast, higher numbers of toad crab (1.35 crabs/stomach) were found in stomachs from cod on rocky and gravel bottom than on mud and sand bottom (0.50 crab/stomach).

There were approximately five times more snow crab (by number) in the stomachs of skate than in cod. The frequency of toad crab present in the stomach contents of both predators was similar. On average, individual skate consumed up to five times more snow crab (by number) than toad crab, while cod consumed approximately equal numbers of toad and snow crab. Estimates of crab abundance provide evidence that cod feed more on toad crab than snow crab, whereas skate seem more opportunistic.

Problems associated with using stomach content analysis to assess the potential impact of cod predation on snow crab recruitment are discussed.

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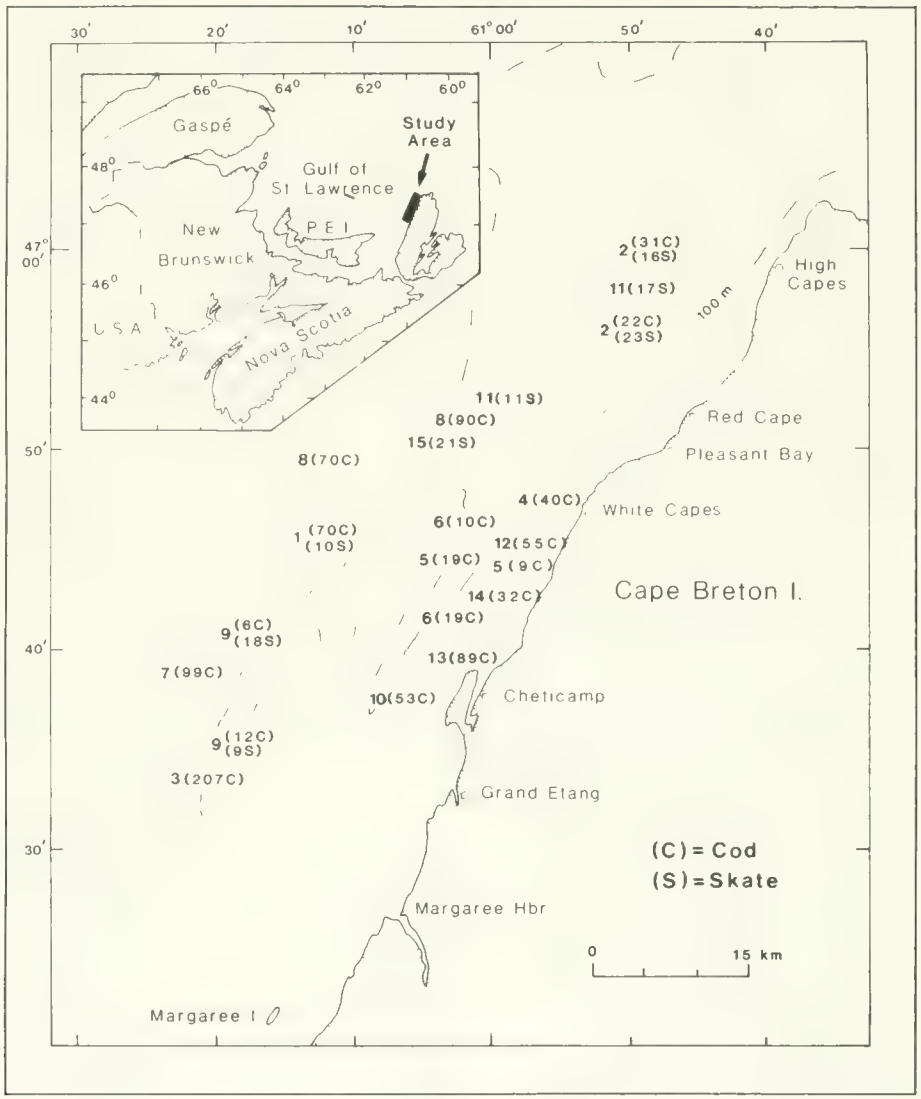
Cod *Gadus morhua* and snow crab *Chionoecetes opilio* which in 1983 supported fisheries valued at $17.4 and $29.1 million, respectively, form two of the most important fisheries in the Gulf of St. Lawrence (Anon. 1982; Elner and Bailey 1986). The snow crab resource is heavily exploited, and the fishery has become almost entirely dependent on the recruitment of crab reaching commercial size each year (Bailey and Elner 1989). Little is known about the factors affecting snow crab recruitment. Past studies on the east coast of Canada have established a predator:prey linkage between cod and snow crab (Waiwood et al. 1980, Waiwood 1981, Bailey 1982, Waiwood and Elner 1982, Lilly and Rice 1983, Lilly 1984, Lilly and Botta 1984, Waiwood and Majkowski 1984). Bailey (1982) suggested that cod predation could be a major factor controlling the number of snow crab entering the fishery each year. However, Waiwood and Elner (1982) suggested that cod do not control recruitment of crab into the fishery, but simply react to the availability of crabs as compared with other prey species.

Although cod has been identified as an important predator of snow crab, the ecological mechanisms involved in the interaction are not well understood. By analyzing cod stomach contents, this work provides fresh insights into cod predation on crab in nature. We also discuss the problems associated with using stomach contents analysis as a means of assessing the impact of cod predation on snow crab recruitment, and evaluate the use of stomach contents as a biological tool for sampling snow crab. For comparative purposes, skate *Raja radiata*, a known predator on crab (Templeman 1982), and two additional crab prey species commonly recognized as toad crab (*Hyas araneus* and *H. coarctatus*) were considered in the study.

Materials and methods

Over the period 21 April 1981 to 29 September 1982, 933 cod and 119

Figure 1
Location of study area and sampling sites during 1981–82. Numbers in parentheses indicate the number of fish sampled, and numbers outside parentheses are sample identification numbers. Data from sites with the same sample number were combined for the analysis.



skate stomachs were collected off the northwestern coast of Cape Breton I. (Fig. 1). Sampling was conducted on an opportunistic basis from various fishing vessels and during research cruises; consequently, different gear types were used (Danish seines, jigs, gillnets, trawls) (Robichaud 1985). Data from samples collected at adjacent sites, on similar bottom, during the same week period and using the same sampling gear were combined and assigned the same sample number (Fig. 1).

Fork length of cod and total length of skate were measured at sea. However, in samples 3 and 8 where large numbers of cod were caught (207 and 160 cod, respectively), all stomachs were removed but, due to limited time, only a random subsample of cod was measured. Possible differences in mean sizes of cod and skate between samples were tested by a "one-way" analysis of variance combined with a Duncan test (Duncan 1955) after transforming the data with Log(x).

Stomach removal was performed by (1) tying off the anterior part of the stomach with plastic "spaghetti" tubing identified by a specimen number, and (2) separating the esophagus in front of the tubing and cutting the posterior part of the pylorus in order to prevent the loss of stomach contents. Stomachs were then preserved in 4% formaldehyde and seawater and transported to the laboratory for analysis. For each cod and skate, data on capture location, depth, bottom type, and gear type were recorded.

In the laboratory, stomach contents were examined and prey remains identified to the lowest taxonomic level that the state of digestion permitted. Food in each taxon was weighed and its contribution, in terms of percent by weight of the stomach contents, was deter-

mined. All unidentified portions and material such as vegetable matter, stones, and mucous were categorized as "others". Empty stomachs, which accounted for less than 9% of the total stomachs sampled, were not used in the analysis. Crab prey were individually identified to species, weighed, measured [carapace width (CW)] and sexed. For each sample, total number of individuals for each crab species, total weight of individuals, frequency of occurrence, and mean number of crabs per stomach were determined. Size-frequency distributions were constructed for each crab species. Relationship between the carapace width of crab and body length of cod or skate predator was also assessed using scattergram plots.

The bottom substrate was sampled using a Van Veen grab. Substrate characteristics were also based on sediment information, collected also with a Van Veen grab, during a juvenile snow crab survey done concurrently with this study (Robichaud 1985, Robichaud et al. 1989).

Results

The average number of *H. araneus* and *H. coarctatus* per cod stomach was 0.37 [variance (S) 1.04] and 0.42 (S 1.82), respectively. Predation by cod on the two toad crab species followed similar patterns. The average number of both toad crab species per cod stomach was higher on gravel bottom [0.59 (S 1.54) and 0.53 (S 1.69) for *H. araneus* and *H. coarctatus*, respectively] and lower on sand and mud bottom [0.19 (S 0.56) and 0.33 (S 1.93) for *H. araneus* and *H. coarctatus*, respectively]. In addition, the number of both toad crab species per skate stomach was low [0.02 (S 0.02) and 0.06 (S 0.16) for *H. araneus* and *H. coarctatus*, respectively]. Because there was no significant differences ($P>0.05$, using t-test) in number per stomach between the two toad crab species, and because of the large proportion (23%) of toad crabs that was unidentifiable and categorized as *Hyas* species, all toad crabs were combined for the stomach analysis.

There were significant differences ($P<0.05$) in the average size of cod between samples (Fig. 2). There were no significant differences ($P>0.05$) in the mean size of skate between samples (Fig. 2).

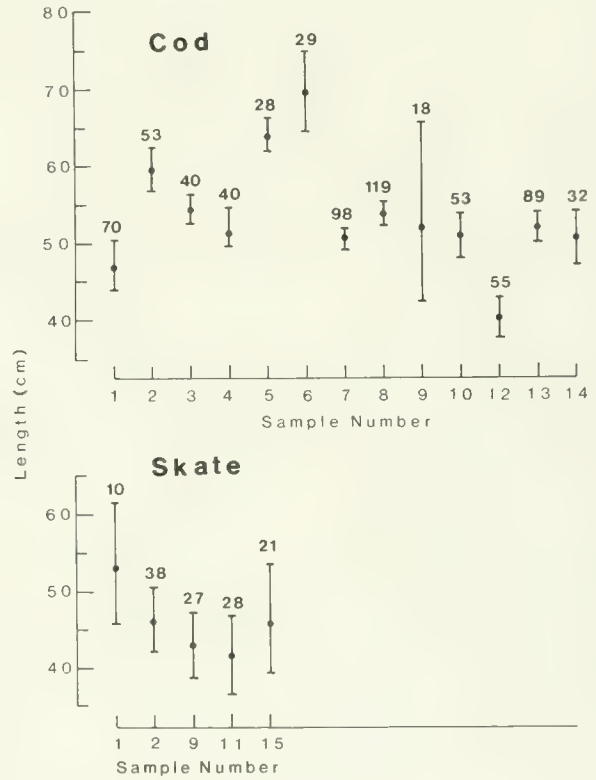


Figure 2

Geometrical mean size of cod and skate for each sample collected during 1981–82. Dots are means; vertical lines are ±95% confidence limits; numbers above dots are the number of fish in each sample.

Cod stomach analyses

The stomach contents of cod caught by Danish seiners or by trawls over deep (100–141 m) muddy or sandy bottoms during the spring of 1981 and 1982 comprised a large percentage by weight of snow crab (Fig. 3; Table 1, samples 1–3). The percentage by weight of snow crab found in cod stomachs ranged between 40.4 and 66.2%. The mean number of snow crab per cod stomach ranged between 0.13 and 0.39, respectively (Fig. 3; Table 1). In the same samples, the percentage by weight of toad crab (*Hyas araneus* AND *H. coarctatus*, combined) ranged between 1.8 and 5.2%, and the mean number of toad crab per cod stomach ranged between 0.10 and 0.53 (Fig. 3; Table 1). The high percentage of the total weight of snow crab in cod stomachs during spring was mainly made up of large soft-shelled males. Whole soft-shelled crabs were usually found compacted into a single pliable ball in cod and skate stomachs. On removal from the stomachs, they could be unfolded and measured. Other prey taxa identified were invertebrates, such as amphipods, euphausiids, and molluscs, and minor quantities of fish (Fig. 3, samples 1–3).

In May 1982, cod taken by jigging over gravel bottom at shallow depth (55 m) contained a negligible amount of snow crab (0.4% of overall weight) (Fig. 3, sample 4). In the same sample, the percentage by weight of toad crab was higher (27.8%) and the mean

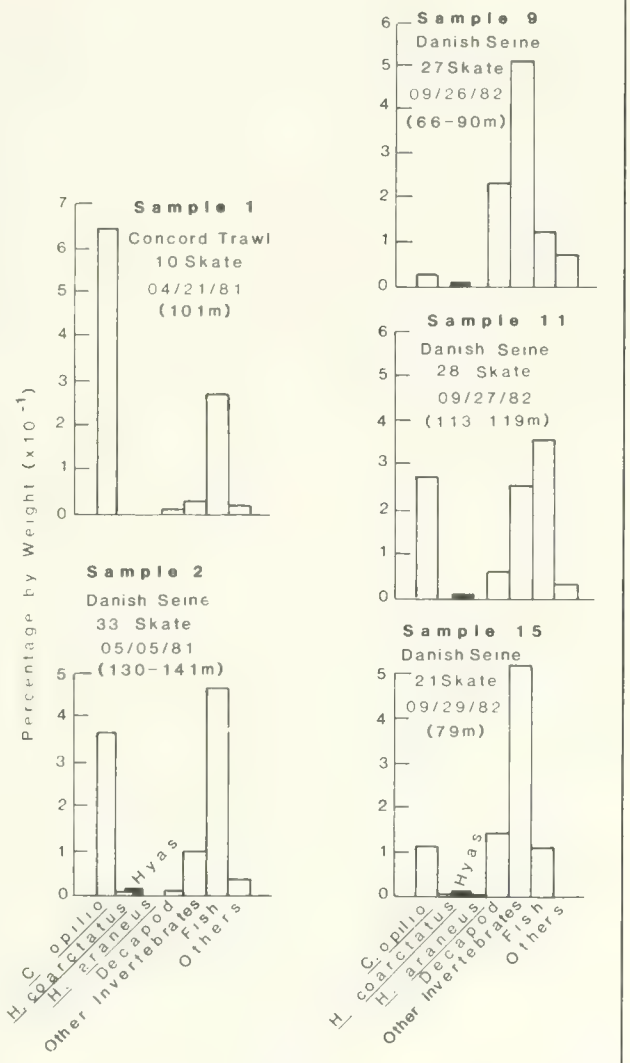


Figure 3

Percentage by weight of prey categories against total weight of stomach contents from cod sampled in April/May 1981 and May 1982. Dark bar represents the percentage by weight of toad crabs (*Hyas araneus*, *H. coarctatus*, unidentified *Hyas*); depth range given in meters.

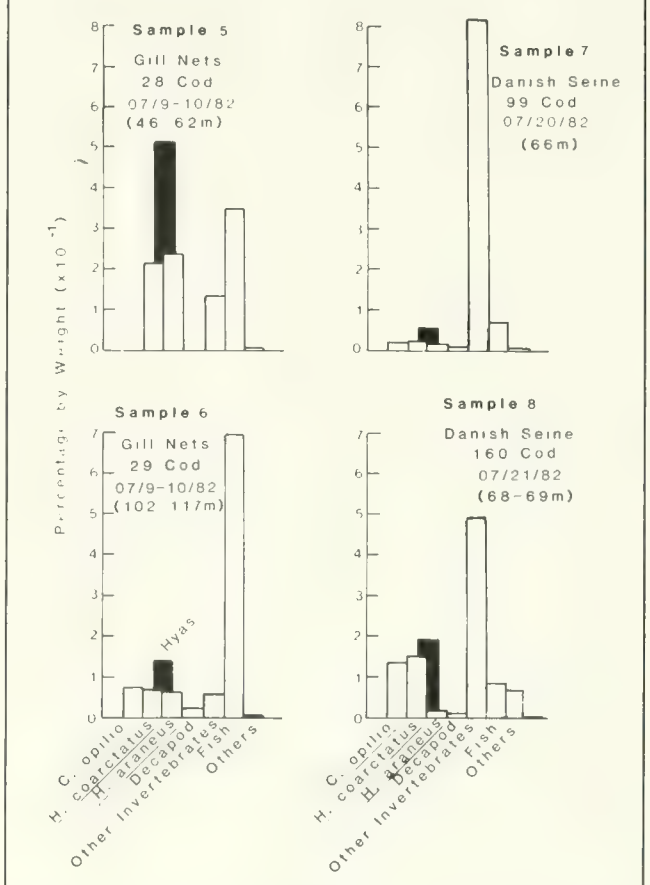


Figure 4

Percentage by weight of prey categories against total weight of stomach contents from cod sampled in July 1982. Dark bar represents the percentage by weight of total toad crabs (*Hyas araneus*, *H. coarctatus*, unidentified *Hyas*).

number of toad crab per stomach was 1.63, compared with 0.05 for snow crab (Fig. 3; Table 1). In this sample, there was also a large proportion (39.9%) of other invertebrates consumed.

During July 1982, in cod sample 5, taken with gillnets set on gravel bottom in shallow water (46–62 m), there were no snow crab (Fig. 4). However, the percentage by weight of toad crab was 51.2%, and the average number of toad crab per cod stomach was 2.0. For sample 6, from the stomach contents of cod also captured by gillnets, but in deeper water (102–117 m) on mud bottom mixed with boulders, the percentage by weight of snow crab was 7.4% and the mean number of snow crab per cod stomach was 0.17 (Fig. 4; Table 1). In comparison with sample 5, the percentage by weight of toad crab in sample 6 decreased to 14.7% and the mean number of toad crab per cod stomach was 1.65 (Fig. 4; Table 1). In cod samples 5 and 6, the major diet percentages of total weight were fish (34.7 and 69.6%, respectively) such as pleuronectids and gadids (Fig. 4).

In July 1982, for stomachs of cod taken by Danish seiners over shallow (66–69 m) sandy and muddy bottoms (Fig. 4, samples 7 and 8), the percentage by weight of snow crab was 2.2 and 13.8%, respectively. This percentage of total weight was lower than that found in cod stomachs taken on similar but deeper (101–141 m) bottoms during spring 1981 and 1982 (Fig. 3, samples 1–3). However, the mean number of snow

Table 1

Snow crab *Chionoecetes opilio* and toad crab *Hyas araneus* and *H. coarctatus* occurring in cod stomachs (with food).

Sample no.	Depth (m)	Date (MDY)	Stomachs sampled	Percentage by weight		Frequency of occurrence		Mean number per stomach	
				Snow crab	Toad crab	Snow crab	Toad crab	Snow crab	Toad crab
1	101	04-21-81	70	40.4	5.2	8.6	4.3	0.13	0.10
2	130–141	05-05-81	53	59.2	4.5	26.4	13.2	0.38	0.53
3	101	05-10-82	207	66.2	1.8	33.3	8.7	0.39	0.19
4	55	05-28-82	40	0.4	29.8	2.5	36.9	0.05	1.63
5	46-62	07-9/10-82	28	—	51.2	—	53.6	—	2.00
6	102–117	07-9/10-82	29	7.4	14.7	10.3	48.3	0.17	1.65
7	66	07-20-82	99	2.2	5.7	30.3	18.2	0.47	0.37
8	69	07-21-82	160	13.8	18.1	52.5	42.5	1.16	1.16
9	66–90	09-26-82	18	24.5	16.1	27.8	16.7	0.78	0.22
10	51	09-26-82	53	0.1	40.8	7.5	52.8	0.08	1.57
12	46	09-27-82	55	—	48.8	—	49.1	—	1.96
13	46	09-28-82	89	0.1	5.5	1.1	27.8	0.01	0.49
14	33	09-28-82	32	—	9.7	—	25.0	—	0.78

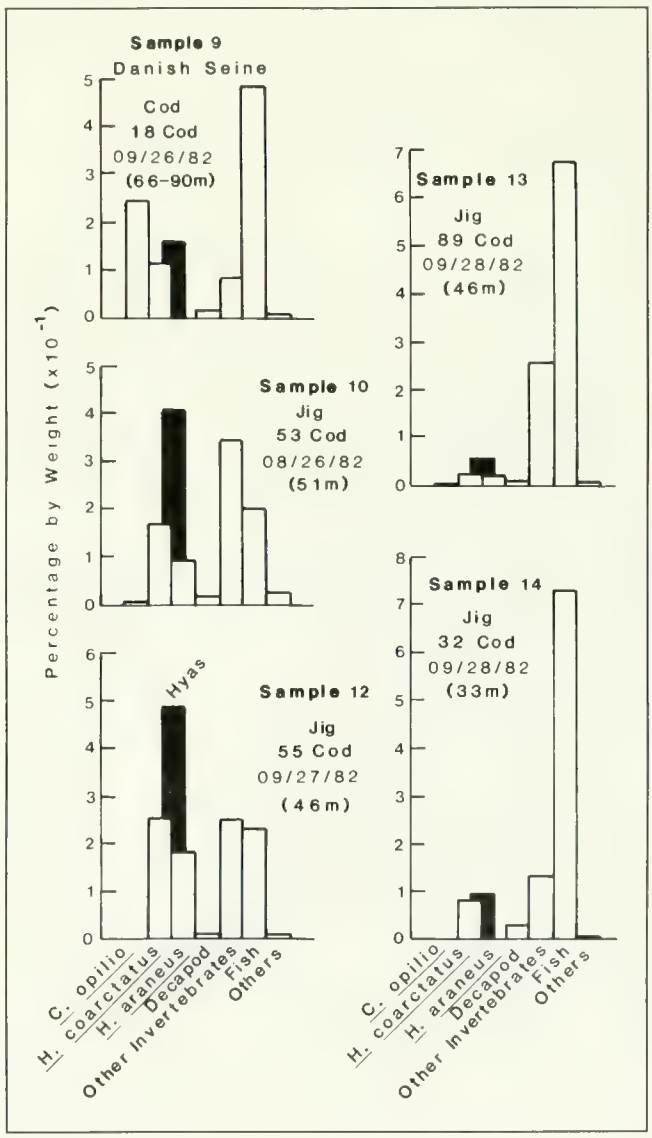


Figure 5

Percentage by weight of prey categories against total weight of stomach contents from cod sampled in September 1982. Dark bar represents the percentage by weight of total toad crabs (*Hyas araneus*, *H. coarctatus*, unidentified *Hyas*).

crab per cod stomach for samples 7 and 8 had increased to 0.47 and 1.16, respectively (Table 1). The percentage by weight of toad crab in cod samples 7 and 8 was 5.7 and 18.1%, respectively. The mean number of toad crab per cod stomach (0.37 and 1.16 crab/stomach, respectively) was similar to the mean number of snow crab found in the same cod stomach samples (0.47 and 1.16 crab/stomach, respectively) (Fig. 4; Table 1). In samples 7 and 8, cod had concentrated their feeding on other invertebrates (49.7 and 82%, respectively) such as euphausiids, gastropods and polychaetes.

During September 1982, in cod sample 9, taken by Danish seiners on muddy or sandy bottom at intermediate depths (66–90 m), the percentage by weight of snow crab was 24.5%, and the mean number of snow crab per stomach was 0.78 (Fig. 5; Table 1). The increase in the percentage by weight of snow crab in September is a consequence of a size increase of juvenile crab ingested in September (13.2 g/crab) compared with July (3.7 g/crab). The percentage by weight of toad crab in sample 9 was 16.1%, and the average number of toad crab per cod stomach was 0.22 (Fig. 5; Table 1). The largest percentage of total weight in sample 9 was composed of fish (48.6%) such as mackerel *Scomber scombrus*, pleuronectids, and smaller gadids.

Cod captured with jigs at sites a few kilometers from shore on shallow (46–51 m) gravel bottom (samples 10 and 12) consumed negligible amounts of snow crab (Fig. 5; Table 1). In contrast, the percentage by weight of toad crab in samples 10 and 12 was 40.8 and 48.8%, respectively, and the mean number of toad crab per cod stomach was 1.57 and 1.96, respectively (Fig. 5; Table 1). Other important prey in the diet of these cod were invertebrates (25.4 and 34.7%) (amphipods, euphausiids, and molluscs) and fish (20.2 and 23.3%) [pleuronectids, mackerel *Scomber scombrus*, and small gadids].

Cod captured with jigs at sites closer to shore on shallower (33–46 m) gravel bottom (samples 13 and 14) also consumed negligible amounts of snow crab (Fig. 5; Table 1). However, the percentage by weight of toad crab was lower, 5.5 and 9.7%, as was the mean number per stomach, 0.49 and 0.78 (Fig. 5; Table 1). In addition, stomachs contained *Cancer* crab and a lobster *Homarus americanus*, but the main prey once again was fish (67.7 and 73.2%) (Fig. 5).

Skate stomach analyses

All skate were collected during spring 1981 and fall 1982 by Danish seines or concord trawls over sandy and muddy bottoms (Fig. 1) (samples 1, 2, 9, 11, and 15). During spring 1981 (samples 1 and 2), the percentage by weight of snow crab found in skate stomachs was 37.7 and 64.3%, and the mean number of snow crab per stomach was 0.30 and 2.26 (Fig. 6; Table 2). The large percentage by weight of snow crab present was large soft-shelled males. Besides crab, skate fed on fish (27.4 and 46.9%) such as cod, hake *Urophysis tenuis*, herring *Clupea harengus*, and sand lance *Ammodytes americanus*.

During September 1982 (samples 9, 11, and 15), the percentage by weight of snow crab had decreased to between 3.5 and 27.6%, but the mean number of snow crab per skate stomach had increased to between 1.44 and 4.81 (Fig. 6; Table 2). The overall average number of crab per stomach was twice as high during the fall as in spring. During fall 1982, skate diet also included large quantities of other invertebrates (up to 52%) (polychaetes, amphipods, euphausiids, gastropods, cephalopods, hermit crab *Pagurus longicarpus*, and brittle stars *Ophiopholis aculeata*) and fish (up to 35%) (Fig. 6) such as mackerel *Scomber scombrus* and pleuronectids.

Comparisons between cod and skate as crab predators

The percentage by weight of toad crab in the diet of skate was small (0–1.3%) (Fig. 6; Table 2). However,

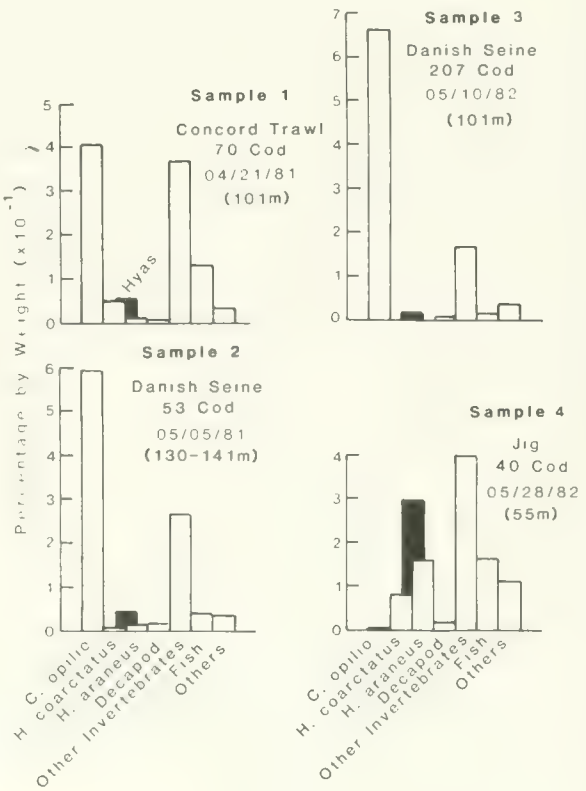


Figure 6

Percentage by weight of prey categories against total weight of stomach contents from skate sampled in April/May 1981 and September 1982. Dark bar represents the percentage by weight of total toad crabs (*Hyas araneus*, *H. coarctatus*, unidentified *Hyas*).

the mean numbers of toad crab per stomach for cod and skate captured at the same sampling sites in the same tows were similar (0.28 and 0.30 for cod and skate, respectively) (Table 3, samples 1, 2, and 9). In these same samples, the mean number of snow crab found in skate stomachs was on average 4.9 times higher than the mean number of toad crab (Table 3), whereas the mean numbers of snow crab and toad crab found in cod stomachs were similar (0.30 and 0.28, respectively). Skate also appeared to consume up to five times more snow crab than cod (1.60 and 0.30 per skate and cod, respectively) (Table 3).

Influence of season and substratum type

The quantity of crab consumed by cod varied between bottom types. In the stomachs of cod captured on sand and mud bottoms, the overall mean numbers of snow crab and toad crab per stomach were generally similar

Table 2

Snow crab *Chionoecetes opilio* and toad crab *Hyas araneus* and *H. coarctatus* occurring in skate stomachs (with food).

Sample no.	Depth (m)	Date (MDY)	Stomachs sampled	Percentage by weight		Frequency of occurrence		Mean number per stomach	
				Snow crab	Toad crab	Snow crab	Toad crab	Snow crab	Toad crab
1	101	04-21-81	10	64.3	—	40.0	—	0.30	—
2	130–141	05-05-81	33	37.7	0.7	75.8	30.3	2.12	0.58
9	66–90	09-26-82	27	3.5	0.2	51.9	14.8	1.44	0.15
11	113–119	09-27-82	28	27.6	0.05	85.7	3.6	4.64	0.04
15	79	09-29-82	21	11.8	0.01	100.0	4.8	4.81	0.05

Table 3

Mean numbers of snow crab *Chionoecetes opilio* and toad crab *Hyas araneus* and *H. coarctatus* per cod and skate stomach for fish captured in the same tows.

Sample no.	Cod			Skate		
	Stomachs sampled	Snow crab per stomach (variance)	Toad crab per stomach (variance)	Stomachs sampled	Snow crab per stomach (variance)	Toad crab per stomach (variance)
1	70	0.13 (0.26)	0.10 (0.29)	10	0.30 (0.45)	—
2	53	0.38 (0.90)	0.53 (3.65)	33	2.12 (5.81)	0.58 (1.12)
9	18	0.78 (3.13)	0.22 (0.30)	27	1.44 (4.04)	0.15 (0.13)
Total	141	0.30 (0.88)	0.28 (1.56)	70	1.60 (4.67)	0.33 (0.62)

Table 4

Mean numbers of snow crab *Chionoecetes opilio* and toad crab *Hyas araneus* and *H. coarctatus* per cod stomach for fish captured by bottom type and seasons.

Season	Sand and mud bottom			Gravel, rocky bottom		
	Stomachs sampled	Snow crab per stomach (variance)	Toad crab per stomach (variance)	Stomachs sampled	Snow crab per stomach (variance)	Toad crab per stomach (variance)
Spring	330	0.35 (0.52)	0.23 (1.12)	40	0.05 (0.12)	1.63 (6.76)
Summer	259	0.90 (1.82)	0.86 (6.97)	57	0.09 (0.18)	1.82 (7.43)
Fall	18	0.78 (3.13)	0.22 (0.30)	229	0.02 (0.02)	1.14 (5.26)
Total	607	0.59 (1.21)	0.50 (3.69)	326	0.04 (0.06)	1.35 (5.86)

except in the fall. However, the fall sample was small (Table 4). On rocky and gravel bottoms, toad crabs were much more abundant (Table 4). Furthermore, the overall mean numbers of snow crab per stomach from cod captured on mud and sand bottoms were substantially greater than for cod captured on gravel and rocky bottoms. For toad crab, mean numbers per stomach were higher in cod captured on rocky and gravel bottom than from sand and mud bottoms.

Crab:cod size relationship

Three distinct size groups of snow crab were detected (Fig. 7). One group, found only during the spring sampling, was comprised mainly of recently molted males ranging in size between 77 and 107 mm CW (Fig. 7). These soft-shelled crabs were consumed by cod ranging in size between 49 and 66 cm (Fig. 7). The second group of snow crab comprised hard-shelled adult females with eggs. This group of crabs was consumed only by larger cod ranging in size between 67 and 106 cm (Fig. 7). The third and most numerous group of

snow crab found in cod was made up of juveniles (of both sexes) ranging between 6 and 44mm CW. These smaller crabs were found in stomachs of cod ranging between 33 and 82cm. The size range of juvenile crab consumed by cod appeared to broaden with cod size (Fig. 7). However, the pattern seems to reach a plateau for juvenile crab above 44mm CW; larger juveniles were not found even in large cod. Larger crab or alternate prey species were present in the stomach contents of cod above 82cm.

The relationship between the size range of the two *Hyas* species and cod length was similar to the relationship found between snow crab and cod (Fig. 8). The size range of toad crab consumed became broader as cod size increased. However, no toad crab over 46mm CW were found.

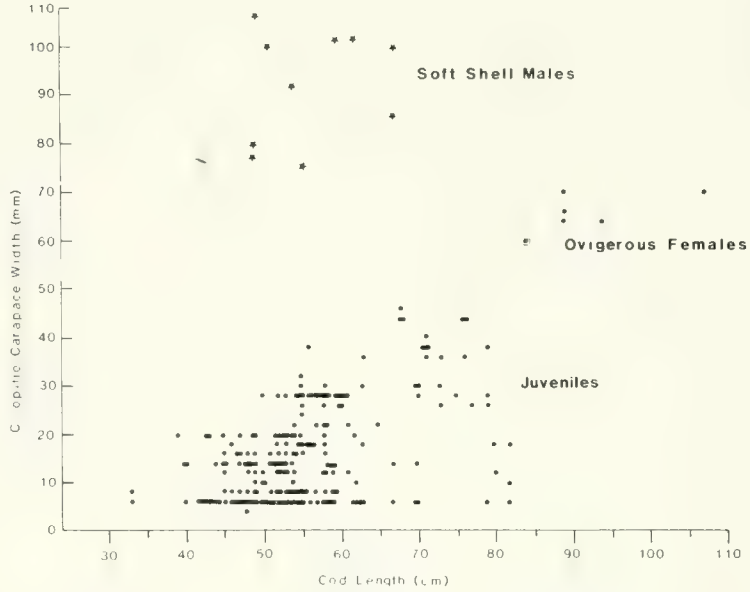


Figure 7

Relationship between carapace width (mm) of *C. opilio* found in the stomachs of cod, and length (cm) of the cod, all cod samples combined for 1981 and 1982.

Crab:skate size relationships

The relationship between skate length and the size of snow crab consumed appears different from the relationship between snow crab and cod (Fig. 7 and 9). The size range of juvenile snow crab consumed by skate is narrower, with no juveniles larger than 27mm CW present, compared with 44mm CW for juvenile crabs found in cod stomachs. Nevertheless, during the spring of 1981, two large soft-shelled male snow crab were found in skate stomachs, indicating that skate were able to feed on larger snow crab (Fig. 9).

The number of toad crab present in skate stomachs was small (Fig. 9). The size range consumed was narrow (5–21mm CW) and did not change with skate size.

Size-frequency distributions of crab prey

By visual inspection, up to six distinct size-classes, or molt groups, were determined for snow crab found in cod stomachs (Fig. 10). Five of these molt groups could be correlated to molt groups determined by Robichaud et al. (1989) for snow crab caught by beam trawling during the same period in the same area. The corresponding mean sizes for each of the molt groups were 6.8, 13.9, 19.6, 27.1, and 37.3mm CW. Only two corresponding molt groups (6.8 and 13.9mm CW) could

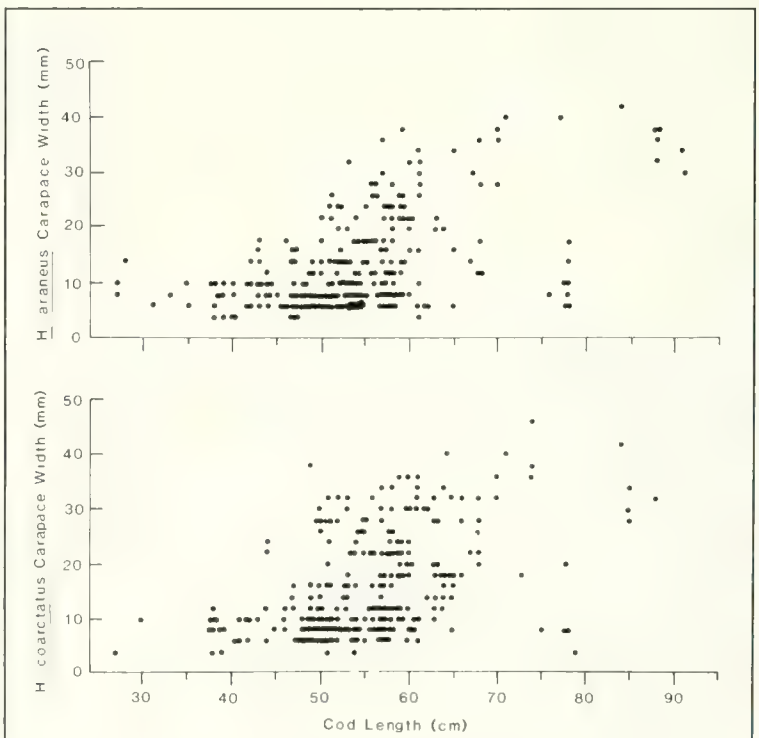


Figure 8

Relationship between the carapace width (mm) of *Hyas araneus* and *H. coarctatus* found in the stomachs of cod, and length (cm) of the cod, all cod samples combined for 1981 and 1982.

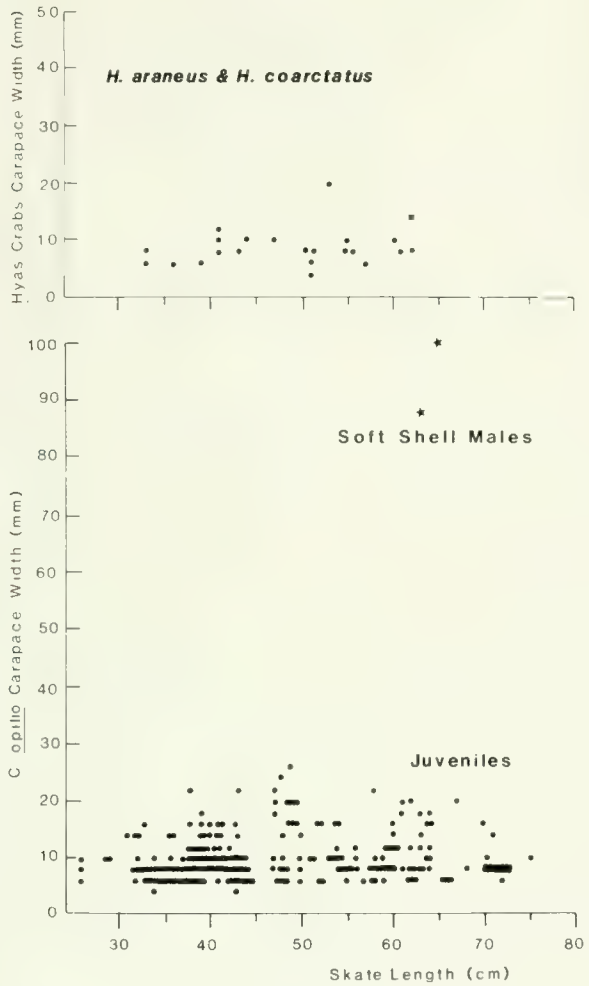


Figure 9

Relationship between the carapace width (mm) of *Hyas araneus*, *H. coarctatus*, and *C. opilio* found in the stomachs of skate sampled in April/May 1981 and September 1982, and the overall length (cm) of the skate.

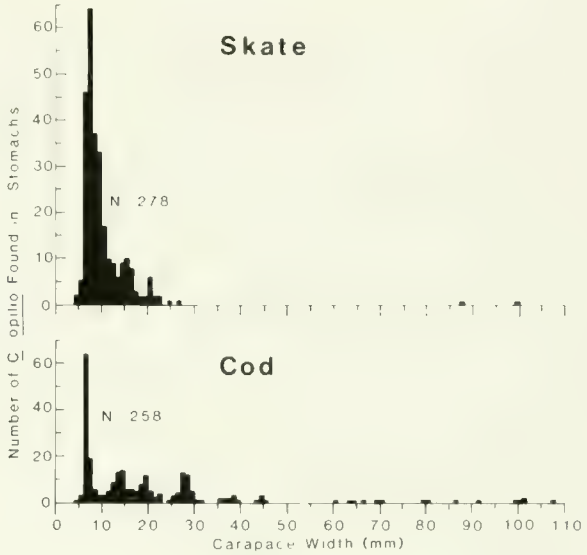


Figure 10

Size-frequency histograms of *C. opilio* found in the stomach contents of all cod and skate sampled in 1981 and 1982.

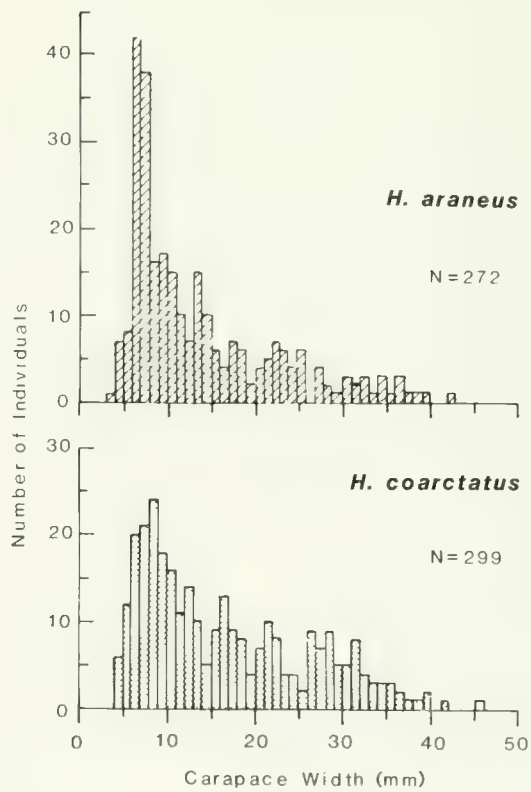


Figure 11

Size-frequency histograms of toad crab found in the stomach contents of all cod sampled in 1981 and 1982.

be identified from snow crab found in skate stomachs (Fig. 10).

The size-frequency distributions of *Hyas araneus* and *H. coarctatus* found in cod stomachs were similar (Fig. 11). However, although molt groups could be determined visually, detailed modal analysis of the distributions was not possible because of the small number of individuals comprising each mode (Macdonald and Pitcher 1979). The maximum size of *Hyas araneus* and *H. coarctatus* found in cod stomachs was 42 and 46 mm CW, respectively.

Discussion

Our study indicates that the diets of cod and skate vary according to season and bottom type. Although there were significant differences ($P<0.05$) in the mean size of cod between some samples which could create some bias in the analyses, the changes in the diet of cod appeared to follow the same general pattern between season and bottom type independent of cod size in each sample (Fig. 2). During spring, cod fed on large soft-shelled male snow crab, while during summer and fall, predation was directed more towards alternate prey species, such as fish and other invertebrates. Seasonal variations in cod diet could reflect the abundance and availability of potential prey species. Such a hypothesis is in accord with Lacroix and Marcotte (1962), Kinnear and Livingstone (1979), Kohler and Fitzgerald (1969), and Corbeil (1954), who argued that seasonal and regional variations in the quantity of prey species eaten by cod are probably due to the distribution of individual prey species, and that prey choice in cod is influenced by prey size, availability, abundance, and ease of capture. Thus, our results may reflect the relative densities and size composition of each crab species present at each sampling site at given times. We found that snow crab were more numerous in cod stomachs from sand and mud bottoms located offshore (0.59 crab/stomach) than on inshore rocky and gravel bottom (0.05 crab/stomach). In contrast, larger numbers of toad crab (1.35 crab/stomach) were found on rocky and gravel bottoms inshore than on mud and sand bottoms offshore (0.50 crab/stomach). We also determined that the two *Hyas* species were present in cod stomachs at similar densities (0.37 *H. araneus* and 0.42 *H. coarctatus*/cod stomach), regardless of bottom type.

Cod and skate appeared to have different feeding patterns for crabs. On average, skate consumed five times more snow crab (1.60 crabs/stomach) than toad crab (0.33 crab/stomach). In contrast, cod captured in the same tows as skate consumed equivalent numbers of snow crab (0.30 crab/stomach) and toad crab (0.28 crab/stomach). Based on a beam trawl survey in the same area during the same periods, Robichaud et al. (1989) determined that snow crab density (11.4 crabs/1000 m^2) was four times higher than the density of toad crabs (2.8 crabs/1000 m^2). If beam trawling is considered to be an unbiased sampling method reflecting the actual densities of both crab species in the area, we can argue that cod feed more on toad crab than snow crab. In contrast, skate would appear to be a more opportunistic predator, feeding on snow crab and toad crab in direct proportion to their actual occurrence.

The stomach contents of cod and skate probably reflect different foraging modes. Cod detect their prey by visual and olfactory cues, but are not capable of detecting buried prey (Brawn 1969). Since snow crab can bury themselves in sediment (Brunel 1960, Miller 1975), cod may experience difficulty in locating them. In comparison, toad crab appear to depend on camouflage rather than burial for protection (D.A. Robichaud, pers. obs.) and are usually found at the sediment surface. As skate prefer foraging in sediment (McEachran et al. 1976), it should be possible for them to detect snow crab buried in mud and sand. In addition, they would also, presumably, be able to locate toad crab on the surface. However, skate may not be as good at catching crabs on the surface.

When attempting to elucidate the impact cod predation could have on snow crab recruitment, many ecological factors need to be considered: distribution patterns of the predator and prey in time and space, size of the predator and prey, availability and vulnerability of the prey, presence of alternative prey species; and behavior of predator and prey. However, one other important non-ecological factor which may influence one's assessment of the relative importance of a prey species in a predator's diet is the method of stomach content analysis employed by the investigator. Different methods of analysis can lead to markedly different conclusions (Hyslop 1980). For example, in this study, if we consider only weight as a measure of the importance of snow crab in cod diet, the greatest quantity of crab present in cod stomachs was during the crab molting period in spring. However, if we consider the actual number of snow crab per stomach or their frequency of occurrence, the number of crab eaten during summer (0.90 crab/stomach) was almost three times higher than spring (0.33 crab/stomach) and the frequency of occurrence was almost twice the spring level (44% vs. 27% in spring). During spring, cod ate fewer but larger soft-shelled male snow crab. During summer and fall, even though the percentage by weight of snow crab was much lower, cod consumed more numerous small juvenile crabs.

Although there are constraints to the present analysis (for example, sampling method, fish size, and the small number of samples), the results provide insight into the predator:prey relationships between fish and crab. However, given the constraints and based on the statistical advice provided, it was decided that any additional effort to statistically isolate the influence of single independent variables such as gear type, season, predator size, depth, or substrate would not only be inappropriate, but liable to create misleading conclusions. For example, studies by Powles (1968), Brêthes et al. (1987), Coulombe et al. (1985), and Robichaud et al. (1989) have shown that substrate is a more important influence than depth on snow crab distribution. We stress that depth, although it may be correlated

strongly with crab density, is secondary to substrate type. Studies by Robichaud (1985) and Robichaud et al. (1989) have shown that snow and toad crab densities were not significantly different over a wide depth range for a given substrate and crab species. A study by Scott (1982) on selection of bottom type by 25 species of groundfish, including cod and skate, concluded, even for species like skate which were not strongly associated to bottom type, that depth was not a specific determinant of distribution.

Previous studies on the impact of cod on snow crab recruitment have not taken into account the behavioral and ecological aspects of the two species (Waiwood et al. 1980, Waiwood 1981, Bailey 1982, Waiwood and Elner 1982). The dynamics of benthos:fish trophic interrelationships are complex, and models based on simple expansion of predator abundance and feeding rate data cannot adequately express the "real world" situation.

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Population Structure, Ageing, and Fishing Mortality of the New Zealand Abalone *Haliotis iris*

David R. Schiel

Ministry of Agriculture and Fisheries, Fisheries Research Centre
P.O. Box 297, Wellington, New Zealand
Present address: Department of Zoology, University of Canterbury
Christchurch 1, New Zealand

Paul A. Breen

Ministry of Agriculture and Fisheries, Fisheries Research Centre
P.O. Box 297, Wellington, New Zealand

Abstract. – Populations of the New Zealand (NZ) black-footed abalone *Haliotis iris* were examined in two important fishing areas. Size-frequencies were compared among three regions around Stewart Island in the extreme south of NZ, three regions of the Marlborough Sounds in the northern part of the South Island, and a site closed to commercial fishing in the North Island. Von Bertalanffy growth parameters were estimated from shell growth rings of subsamples from all regions. Mark-recapture data were available for two regions, and independent estimates of von Bertalanffy parameters were calculated. Total mortality was estimated from catch curves and also from length-frequencies using the method of Fournier and Breen (1983). Yield-per-recruit (YPR) and egg-per-recruit (EPR) were calculated and two reference levels of fishing mortality, $F_{0.1}$ and $F_{25\%}$, were estimated. Analyses showed that, despite previous evidence to the contrary, rings are not laid down annually in the regions we examined. For two fishing regions, the estimated current fishing mortality rates are greater than both $F_{0.1}$ and $F_{25\%}$, suggesting that the current fishery is more intense than can be sustained in the long term. YPR and EPR do not appear to be greatly affected by changing the minimum legal size. By decreasing F to $F_{0.1}$, however, equilibrium egg production would increase from 18% to a more satisfactory level with little change in YPR. We discuss management strategies and argue that it would be prudent to decrease fishing mortality, thereby maintaining higher egg production at little sacrifice of YPR.

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The fishery for the abalone *Haliotis iris* (called "paua" in New Zealand) is now one of the largest abalone fisheries in the world, yet the biological basis for its management has only recently been examined in detail. Both the minimum legal size (MLS) for fishing and the permissible catch level were arbitrarily set for historical reasons that did not take into account the best yield and egg production of the fishery. Recent research has aimed at assessing whether the present levels of fishing are sustainable.

Individual Transferable Quotas (ITQs) for paua were implemented in 1986 and a Total Allowable Commercial Catch (TACC) was set in each of seven Quota Management Areas (QMAs), based on the previous catch histories of commercial fishers (Schiel 1991). The total catch of paua for the entire country is currently 1193 tons (whole weight).

Haliotis iris is a shallow-water species, endemic to New Zealand (NZ). It occurs around the entire coastline, but is most abundant in the cooler waters from Cook Strait southwards. It is found predominantly at depths of <5 m (Schiel, unpubl. data). Fishing is restricted to free-diving, and no underwater breathing apparatus is allowed. Paua reach 195 mm (shell length) and the MLS is 125 mm. The commercial value of the fishery has increased dramatically during the last five years (Schiel 1991). There are also a large recreational fishery and a continuing importance of both paua meat and shell to the indigenous Maori people.

The history of abalone fisheries worldwide shows that management is difficult and that populations are often overfished, causing a precipitous drop in commercial landings (Sloan and Breen 1988). The difficulties in management arise from the spatial patchiness and sedentary nature of abalone (Poore 1972b, Shepherd 1986, Sluczanowski 1986), an uncertain relationship between standing stock and recruitment (Prince et al. 1988, Breen 1991), and often a paucity of useful information on growth and mortality (Shepherd and Breen 1991). These uncertainties also apply to the NZ paua fishery, which occurs over most of the coastline including many remote places with rough sea conditions and difficult access.

Although the fishing of paua goes back to pre-colonial times (Best 1929), there is a relatively small history of research on the fishery (Schiel 1991). Growth and mortality rates have been studied for only a few sites in the South I. (Poore 1972a, Sainsbury 1982). Estimates of basic

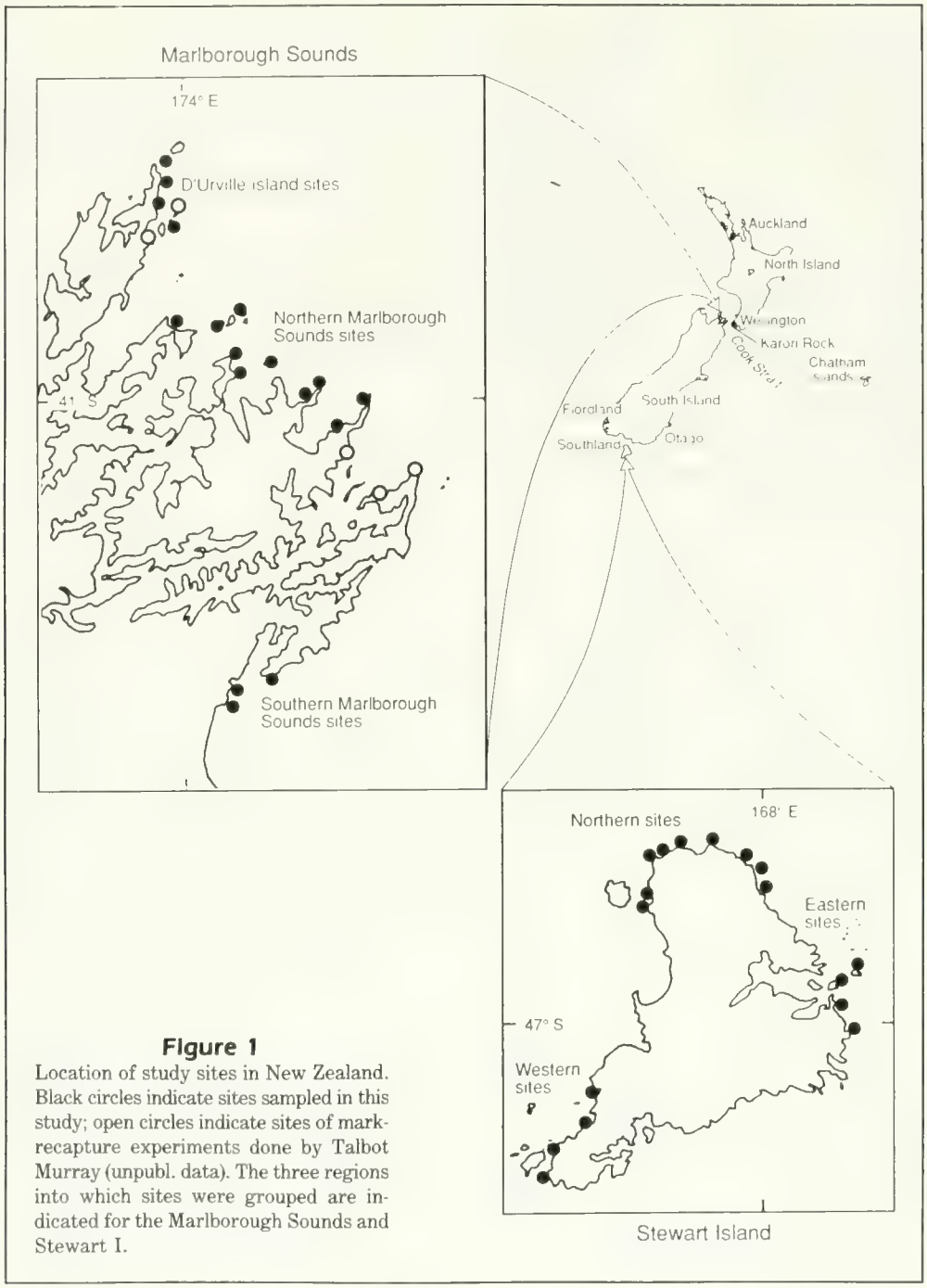

Figure 1

Location of study sites in New Zealand. Black circles indicate sites sampled in this study; open circles indicate sites of mark-recapture experiments done by Talbot Murray (unpubl. data). The three regions into which sites were grouped are indicated for the Marlborough Sounds and Stewart I.

population parameters are required to manage the fishery effectively. In this paper we assess the size structure, age structure, and mortality of paua populations.

We estimate 'age' from growth rings in shells and assess the usefulness of this ageing technique for paua. This is potentially one of the most powerful tools available for estimating growth and mortality rates (Shepherd and Breen 1991). Cross sections of *H. iris* shells have obvious rings. These have previously been used to estimate age and growth (Murray and Akroyd 1984, Murray 1986, Hahn 1989), but no verification has been reported. Similar rings have been used elsewhere to age abalones. For instance, rings in *H. tuberculata* (in the English Channel) have been verified by growth studies (Forster 1967, Hayashi 1980). Verification is also reported in Japanese *H. discus discus* (Kojima et al. 1977) and the Korean *H. diversicolor diversicolor*

and *H. d. aquatilis* (Kim and Cheung 1985). Inoue and Oba (1980) suggest that shell circuli are annual for Japanese *H. gigantea*. Prince et al. (1988) describe a method for ageing Tasmanian *H. rubra*, based on the method of Munoz-Lopez (1976).

In two quota management areas that support substantial landings, we compare estimated levels of fishing mortality with estimates of appropriate levels of fishing mortality obtained from per-recruit modeling. We also compare growth and mortality estimates from shell growth rings with those obtained from other methods. Finally, we explore the consequences of altering the present MLS.

Materials and methods

Field sampling

The size structure of emergent *H. iris* populations was examined around Stewart I., which comprises a major part of the southern fishery, and the Marlborough Sounds, which are a major part of the fishery in the northern part of the South I. (Fig. 1). Stewart I. is exposed to a range of weather conditions. The east coast is in the lee of prevailing westerly winds, but is occasionally subjected to severe easterly storms. The west coast of the island is often inaccessible due to the prevailing winds and a large onshore swell. During the time of our sampling, the swell was reduced to about 1 m. The northern side of the island is protected from the westerly winds but has a refracted westerly swell. Paua occur along the entire coastline of Stewart I.

The Marlborough Sounds are generally less exposed than Stewart I. Paua occur only at the outer margins of the Sounds, as the inner shores are protected and provide generally unsuitable habitat for paua. Northerly winds funnelling through Cook Strait are occasionally severe and can bring exposed conditions to most places where paua are fished. The eastern side of D'Urville I. is protected from westerly winds. Sites in the central portion of the Sounds are generally subjected to similar conditions of exposure to the north, while southeastern sites are protected from the west and north. One other site was used in this study.

Karori Rock is on the south coast of the North I. It is within an area closed to commercial fishing since 1974 after severe depletion of paua populations caused by both commercial and recreational fishing. This site is generally protected from severe swells but occasionally experiences severe northerly and southerly storms in Cook Strait.

Except at Karori Rock, sampling sites were chosen to be representative of commercially harvested sites. This was done in consultation with commercial divers and, at Stewart I., a commercial diver assisted us in the field. During 15–25 September 1989, 17 sites were assessed at Stewart I., and 19 sites during 17–23 October 1989, at the Marlborough Sounds. Karori Rock was sampled on 30 November 1989. Each sampling site was roughly 1 ha in area. Paua were collected, taken to a boat, measured to the nearest mm (shell length), and a subsample from each site was frozen and taken back to Wellington for weighing and ring counting. Remaining paua were returned to their habitat. The numbers collected at each site varied (range 125–548), depending on sea conditions and the abundance of paua. The goal was to collect several hundred paua at each site. To remove paua, we used a blunt trowel of a type commonly used by commercial divers, and took care not to cause damage. Paua less than 70 mm were not representatively sampled because they occupy cryptic inshore habitats and require different sampling techniques. We attempted to sample paua >70 mm representatively by having each diver remove all paua as they were encountered. A total of 5790 (Stewart I.) and 8731 (Marlborough Sounds) paua were measured.

For analyses, we grouped sites by regions of Stewart I. and the Marlborough Sounds (Fig. 1) because we did not wish to assess fine-scale variability in parameters.

Ageing and growth

Shells in the ring-count subsample were measured in length and then sectioned sagittally through the spire with a lapidary saw. Because the rings are obvious (Fig. 2) no further enhancement was necessary. Ring counts for all shells were done by the same experienced technician.

From the ring-count sample data we estimated the von Bertalanffy growth parameters with the non-linear least-squares procedure FISHPARM (Saila et al. 1988). We also estimated growth parameters from mark-recapture data obtained at several sites (Fig. 1) in the northern Marlborough Sounds and around D'Urville I. (Talbot Murray, Min. Agric. Fish., P.O. Box 297, Wellington, pers. commun.). Abalone had been collected, tagged with a numbered plastic disc attached to the shell with epoxy putty, replaced, and recovered later. Most of the times-at-liberty were one year; increments for shorter and longer times (range 92–519 days) were adjusted *pro rata*. We estimated asymptotic length L_∞ and the Brody growth coefficient K from a Ford-Walford regression (Ricker 1975). For comparison with these results, we also calculated growth parameters from age estimates (ring counts) obtained from abalone in the same experiments (Talbot Murray, pers. commun.). The ring counts were done by the same technician, as explained above.

Figure 2
Growth rings in a cross section of a *Haliotis iris* shell.

Mortality estimation

Age-length keys (Ricker 1975) were constructed from the ring-count data. The keys were used to estimate the catch curve from the length-frequency sample for each region; total mortality rate was then estimated from the regression of the natural log of estimated number-at-age on 'age' (Robson and Chapman 1961). The first 'age' included in the procedure was chosen to represent the first 'age' class with a mean length greater than minimum legal size.

Total mortality rates were also estimated from the length-frequency samples using the method of Fournier and Breen (1983), using a strategy similar to that of Tegner et al. (1989). To obtain the fishing mortality rate F, we subtracted an assumed value of $M = 0.10$, based on the work of Sainsbury (1982), from the total mortality rate Z. Natural mortality rate is difficult to estimate, especially in fished populations (Shepherd and Breen 1991); Sainsbury used several methods to estimate M in a population protected from fishing. The method of Fournier and Breen (1983) can estimate growth and mortality rates simultaneously but is better applied by constraining the growth estimates, to be consistent with independent estimates. We applied this method to length-frequencies from the northern Marlborough Sounds and D'Urville I., using the growth estimates obtained from mark-recapture data in those regions. This method could not be applied to the other regions because we had no independent estimates of growth.

In using the Fournier and Breen (1983) method, the assumed number of age classes N was determined by examining results using different values of N. We chose the highest value for which the procedure estimated a substantial proportion of the population to be contained within each age-class. At unrealistically high values of N, the procedure estimates that some age-classes are "empty." The parameter NFULL (the index of the first cohort whose abundance is used in estimating mortality) was chosen with reference to the mean cohort length and the minimum legal size. Estimated standard deviations of lengths-at-age around mean length-at-age were constrained to values near 4.1, based on examination of length-frequencies in which cohort modes were clear (Schiel, unpubl. data). L_∞ was unconstrained except for D'Urville I., where a minimum constraint was required to obtain estimates consistent with the mark-recapture data. Population proportions were left unconstrained unless the procedure made unrealistically high estimates for single age-classes. Variance of mean lengths from the von Bertalanffy growth curve and variance of the estimated population proportions from an exponential decay curve were both constrained to a maximum of 1.0. Sensitivity of the procedure to changes in N, NFULL, K, and the standard deviations of length-at-age was examined by varying these parameters (see Tegner et al. 1989).

Modeling

Yield-per-recruit (YPR) modeling was done on a spreadsheet incorporating the YPR model of Ricker (1975). We report results from two regions: the northern Marlborough Sounds and D'Urville I. Length-weight relations were calculated from field sampling results (Table 1). Egg production modeling was done for these regions using a simple spreadsheet model of the form described by Sluczanowski (1984, 1986). The additional information required for this modeling is the length-fecundity relation. Relevant data are available from Poore (1973), Sainsbury (1982), and Wilson (1987). Based on the size range of paua in each of these sources, we used Wilson's data to derive

$$\text{Eggs} = (9.32 \times 10^{-12}) \times \text{shell length (mm)}^{8.408}.$$

The natural mortality rate M was assumed to be 0.10. We assessed the sensitivity of the results to this assumption by varying M. For the northern Marlborough Sounds, we also varied M and the size-at-first-capture and developed the response surface of YPR

Table 1
Length-weight power curves for each of the regions of New Zealand examined. The relation is whole weight (g) = a × (length (mm)^b).

Region	*n*	a	b
Karori Rock	278	3.593E-5	3.305
Stewart I. West	495	5.308E-5	3.169
Stewart I. North	416	3.918E-6	3.718
Stewart I. East	499	2.994E-5	3.303
Marlborough D'Urville	335	2.592E-5	3.322
Marlborough North	497	2.470E-5	3.339
Marlborough South	181	4.927E-5	3.190

and egg production. For each region, the von Bertalanffy growth curves from mark-recapture data were used.

We held the age-at-first-capture constant at the first age-class with a mean length equal to or greater than 125 mm. Then we varied the instantaneous rate of fishing mortality, F, to estimate $F_{0.1}$ and $F_{25\%}$. $F_{0.1}$ is the fishing mortality rate at the point where yield-per-recruit increases with F one-tenth as fast as it does at the origin. Although arbitrary, $F_{0.1}$ is used by several major international stock assessment agencies as a guide to appropriate target fishing mortalities (Mace 1988). $F_{25\%}$ is the fishing mortality rate at which equilibrium egg production is 25% that of an equilibrium virgin population.

Results

Field sampling

Haliotis iris were abundant at all sites, despite more than 30 years of commercial fishing activity in all regions. It was not our intention to estimate densities, but an indication of abundance is given by the length of time it took to obtain our samples. The mean was 155 paua per diver-hour (SD 33.6) or about 32 kg whole wt per diver-hour.

The structure of paua populations varied considerably among the seven regions (Fig. 3). The three regions of Stewart I. show clear differences in the modes (Fig. 3A–C). The west coast region had the major mode at 140–145 mm shell length, well beyond the minimum legal size of 125 mm, and paua were found up to 187 mm. The major mode for the northern region was at 125–130 mm. The east coast region had a higher proportion of smaller paua and the major mode was at 120 mm.

In contrast to Stewart I., length-frequencies for the three regions of the Marlborough Sounds were similar to one another (Fig. 3D–F). The major modes were around 125 mm (MLS), and smaller paua were found in each region. There has probably been roughly similar fishing pressure in these three regions in recent times.

Although the Karori Rock site is closed to commercial activity, it is subjected to considerable illegal fishing (Schiel 1989). The major mode in length-frequency is at 130 mm (Fig. 3G). Because illegal fishing removes paua of all sizes, it reduces paua densities but does not necessarily change the population size structure.

Ageing and growth

A typical ring-count frequency is shown for the Marlborough Sounds D'Urville I. region (Fig. 4). Paua appear to be fully recruited to the sampling procedure by 'age' 10. The greatest ring count we observed was 34 at the west coast of Stewart Island. Growth rates were obtained from the ring count data for all sites (Table 2). Growth parameters from ring-count data and mark-recapture experimental data for two regions (Table 3) and the mean increments predicted from the two methods (Fig. 5) were compared. A large difference between the two methods was evident: the mark-recapture data resulted in higher K estimates and larger L_∞ estimates; estimated growth from mark-recapture data was much greater than from ring-count data. This pattern is the converse of what would be expected if the tagging procedure had retarded growth; therefore, we consider the mark-recapture data to be more reliable. The mark-recapture data are inconsistent with the assumption that one, or even two, rings are laid down annually.

Mortality estimation

Total mortality rates from the catch-curve analyses ranged from $Z = 0.216 - 0.425$ (Table 4). Mortality estimates based on the length-frequency analysis, and the parameters used to obtain them, are shown in Table 5. The estimates varied when N, NFULL, K, and the standard deviation constraints were varied; the pattern of change was not consistent between data sets. Only variation in N caused large variation in estimated Z. The Methods describe an objective procedure for choosing N. The 'best' estimates (using the criteria described above) were $Z = 0.495$ and $Z = 0.507$ for the northern Marlborough Sounds and D'Urville regions, respectively. The extreme range observed over all parameter variations in the two data sets was $Z = 0.238 - 0.995$.

Modeling

Growth rates used in modeling were those estimated from mark-recapture data (Table 3) for the northern

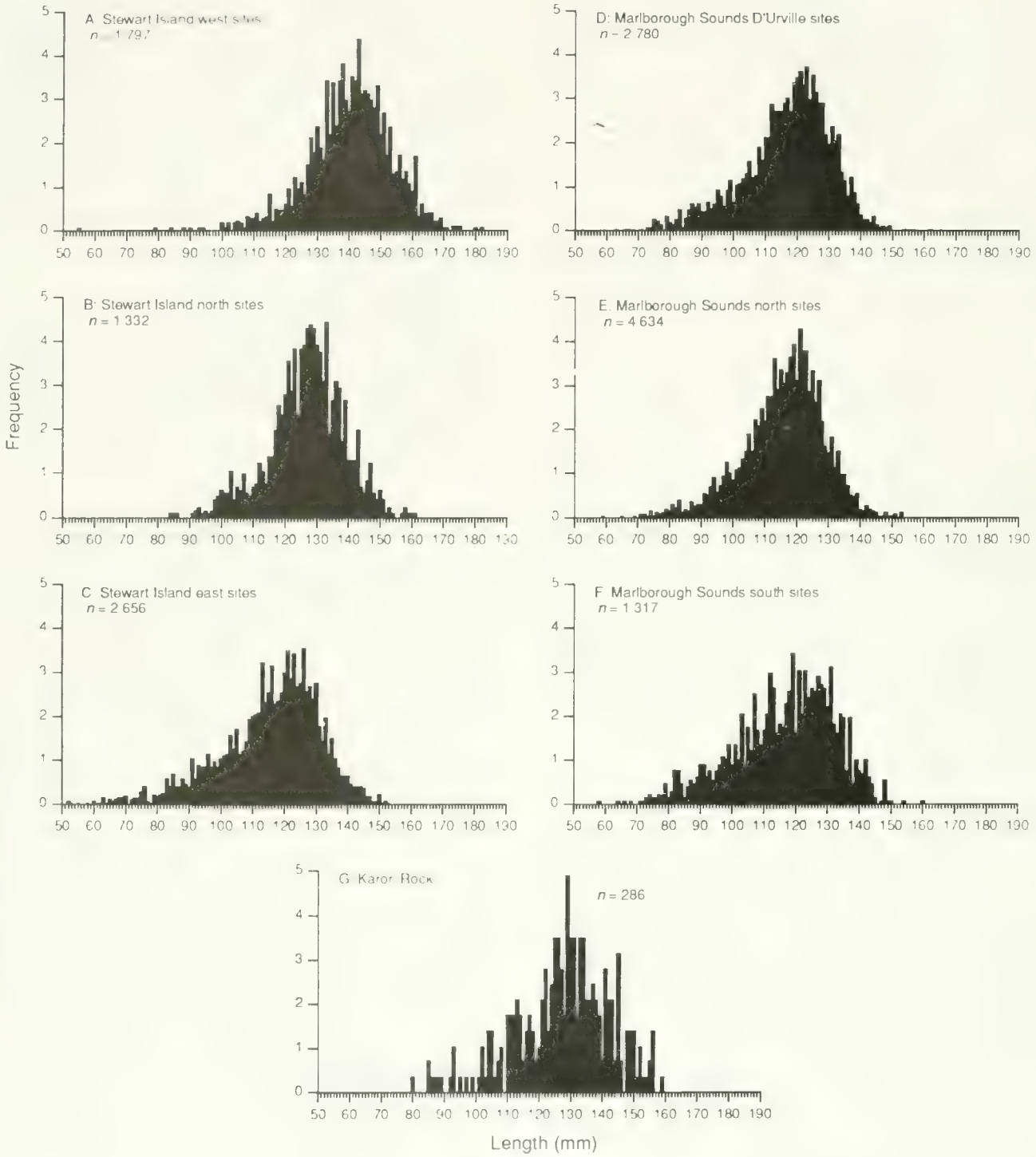

Figure 3
Size-frequency histograms of *Haliotis iris* measured in September and October 1989.

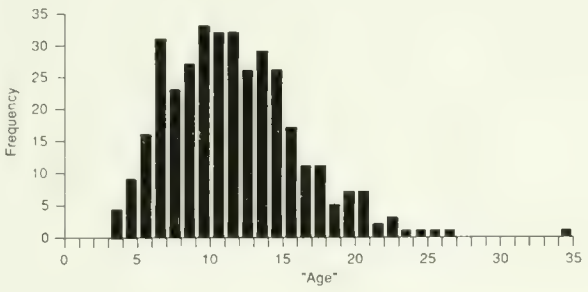

Figure 4

'Age' estimates from growth ring counts (n 335) in one region (Marlborough Sounds D'Urville I.), assuming that one growth ring represents one year of age.

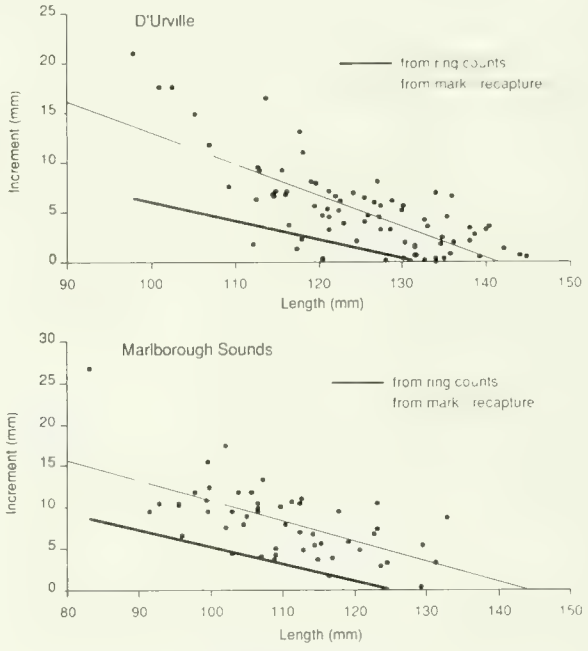

Figure 5

A comparison of the length-specific growth increments predicted from the mark-recapture data (thin line) and from growth ring counts (thick line) in two regions of the Marlborough Sounds. Data points are the observed growth increments; predictions were based on data in Table 3.

Marlborough Sounds and D'Urville I. regions. Growth estimates from ring count data were not used because of the discrepancy seen in Table 3. Estimates of $F_{0.1}$ and $F_{25\%}$ resulting from YPR analyses are given in Table 6 for three assumed M values. In all cases, $F_{25\%}$ was greater than the estimated $F_{0.1}$ obtained from the same parameters.

The best estimates of actual fishing mortality rates, obtained from the procedure shown in Table 5, were substantially higher than $F_{0.1}$ in both regions examined (Table 6). This result is not sensitive to the assumed M, although higher M values increase $F_{0.1}$ and decrease the estimated current level of F. Response surfaces in YPR and egg production resulting from variation in M and the size-at-first capture are shown in Figures 6 and 7, respectively. These show the typical form of such surfaces (cf. Tegner et al. 1989). When M is higher, maximum YPR is obtained at a lower size for a given F, or at a higher F for a given size. Egg production follows a simpler pattern, but is greater at a given combination of F and size-at-first-capture when M is greater. Yield and egg production resulting from different values of M and MLS are shown in Table 7.

Table 2

Estimates of von Bertalanffy growth parameters (with standard errors) from the growth ring-count data of *Haliotis iris* where L_∞ is the asymptotic length, K is the Brody coefficient (Ricker 1975), and t_0 is the theoretical age at length zero.

Region	n	L_∞	K	t_0
Karori Rock	278	143.2 (2.41)	0.160 (0.022)	−8.4 (0.96)
Stewart I. West	495	153.3 (1.63)	0.143 (0.017)	−7.0 (1.17)
Stewart I. North	416	134.1 (0.81)	0.318 (0.034)	−5.9 (0.54)
Stewart I. East	499	130.9 (1.21)	0.283 (0.027)	−6.0 (0.43)
Marlborough D'Urville	335	131.1 (1.79)	0.210 (0.022)	−6.6 (0.53)
Marlborough North	497	135.0 (3.06)	0.114 (0.018)	−11.5 (1.47)
Marlborough South	181	134.8 (2.68)	0.291 (0.042)	−4.7 (0.51)

Table 3

A comparison of von Bertalanffy growth parameters estimated from growth ring-count data from several sites in the D'Urville I. and northern Marlborough Sounds regions (Fig. 1) and mark-recapture data from experiments at the same sites (Talbot Murray, unpubl. data). Sample sizes are unequal because more animals were subjected to ring counting than marks were recovered.

	Mark-recapture data			Ring-count data				
Place	n	L_∞	K	n	L_∞	(SE)	K	(SE)
D'Urville I.	79	141.6	0.379	131	131.5	(2.21)	0.197	(0.029)
Northern Marlborough	53	144.5	0.285	180	126.4	(2.65)	0.214	(0.052)

Discussion

Size structure

Evidence from length-frequencies indicates that in some regions the fishery may still be sustained by the accumulated stock. Although reliable catch-per-unit-effort figures are not available for the commercial fishery, it is probable that the west coast of Stewart I. represents such a region. The weather and sea conditions render this region inaccessible for much of the year, but it is a favored place to fish when conditions permit because of the large sizes and abundance of paua. In contrast, sites on the east coast of Stewart I. are considerably more sheltered, generally accessible to fishing, and closer to a port. The observed population structure in the eastern region, with most paua below MLS, is consistent with a population in equilibrium with the fishery.

There are alternative explanations for the differences in size-frequencies. One possibility is a difference in growth rates among regions: L_∞ could be smaller in the eastern region of Stewart I. than the western region. Another possibility is that the population structure seen at the west coast of Stewart I. may have resulted from a short period of good recruitment followed by poor recruitment. A third possibility is that natural mortality is much higher in the eastern region of Stewart than in the other regions. Similarly, population size structures seen in the Marlborough Sounds could be explained by high natural mortality, recruitment variation, or stunted growth in some regions. Only repeated

Table 4

Total mortality estimates, and their standard errors, from the catch curve method, based on growth ring-count data. Sample sizes are given for the ring-count and length-frequency samples.

Region	Ring-count sample	Length sample	Z (SE)
Karori Rock	285	285	0.16 (0.022)
Stewart I. West	319	1796	0.13 (0.017)
Stewart I. North	412	1332	0.19 (0.022)
Stewart I. East	313	2662	0.28 (0.031)
Marlborough D'Urville	173	2780	0.38 (0.049)
Marlborough North	263	4634	0.36 (0.060)
Marlborough South	90	1317	0.25 (0.050)
Total	1855	14806	

Table 5

Estimates of total mortality rate Z based on length-frequencies, using the method of Fournier and Breen (1983). N is the assumed number of age classes; NFULL is the number of the first age-class included in the mortality estimate; "SDevs" are the standard deviations of lengths in the first and last age-classes; T is the value of the objective function minimized by the procedure. Asterisks indicate constrained values.

Region	N	NFULL	SDevs		L_∞	K	T	Z
Northern Marlborough Sounds	14	7	4.1*	4.2*	144.4	0.28*	92.8	0.49
D'Urville I.	12	6	4.2*	4.2*	138.0	0.37*	162.0	0.51

Table 6

Comparison of estimated fishing mortality rates (F) with the reference levels $F_{0.1}$ and $F_{25\%}$ for two regions, and sensitivity of the estimates to assumed natural mortality rate M.

Region	$F_{0.1}$	$F_{25\%}$	Est. F
Northern Marlborough Sounds			
M = 0.05	0.11	0.16	0.45
M = 0.10	0.18	0.27	0.40
M = 0.15	0.25	0.47	0.35
D'Urville I.			
M = 0.05	0.11	0.18	0.46
M = 0.10	0.18	0.32	0.41
M = 0.15	0.27	1.11	0.36

Table 7

Northern Marlborough Sounds region: YPR (top) and egg production (bottom) for three different levels of assumed M, for three different minimum legal sizes. YPR is in grams whole weight; egg production is expressed as a percentage of the eggs produced by a virgin population.

MLS	115		125		130	
M	F_{est}	$F_{0.1}$	F_{est}	$F_{0.1}$	F_{est}	$F_{0.1}$
0.05	219.0	196.1	230.6	199.0	236.5	205.4
0.10	175.9	151.1	176.2	151.1	171.9	147.0
0.15	139.0	126.3	132.5	122.2	122.9	114.4
0.05	7.4	33.4	9.9	35.0	12.8	34.1
0.10	14.0	31.1	18.1	33.3	12.5	36.6
0.15	22.6	31.1	28.2	34.6	33.9	39.1

Figure 6
Yield-per-recruit as a function of the natural mortality rate (M), fishing mortality rate (F), and the minimum legal size. In A, M = 0.05; B, M = 0.1; C, M = 0.15.

Figure 7
Egg production as a function of the natural mortality rate (M), fishing mortality rate (F), and the minimum legal size. In A, M = 0.05; B, M = 0.1; C, M = 0.15.

sampling through time, and appropriate experimentation, can distinguish among these alternatives.

Ageing and growth

Despite the fact that growth rings in *H. iris* are quite distinct, as has been reported for other species (Prince et al. 1988), they are evidently not annual in at least some populations. Predicted growth increments from ring count data were much less than observed increments from mark-recapture. This suggests that more than one ring is laid down annually, but it is not clear whether the deposition of growth rings follows a regular annual pattern. We examined the hypothesis that the growth rings are semi-annual, but predicted and observed growth increments still did not agree. Consequently, the ring counts overestimate age in two study regions. This appears to be borne out by length-frequency analysis of mortality in which the estimates are higher than those from catch curves.

Our experience underscores the need to validate age estimates from independent data (Beamish and McFarlane 1983). For *H. iris*, the use of growth rings leads to the erroneous conclusion in at least two populations that they are more lightly fished than indicated by length-frequency analysis based on mark-recapture data.

Mortality

For the reasons discussed above, we consider that the mortality rates based on ring counts are spurious for *H. iris*, at least for the regions examined. Mortality rates derived from length-frequency distributions are heavily dependent on the assumptions of the method. One critical assumption is that recruitment to the population is roughly constant. If recent recruitment has varied with any trend, analysis of a single length-frequency sample cannot provide a realistic estimate of mortality (Shepherd and Breen 1991). We have no data on annual variation of recruitment at our sampling sites. Interannual variation can be high in some species of abalone (Tegner et al. 1989), but it is systematic change in recent recruitment that causes estimates to be dubious. However, it is encouraging that our estimates of mortality are reasonably robust to variation in the input parameters (Table 5).

Other important assumptions are that natural mortality is age-independent (over the age range examined) and also constant for all areas. For abalones generally, the first assumption is not unreasonable for mature animals (Shepherd and Breen 1991) and, for *H. iris*, it is consistent with the conclusions of Sainsbury (1982). Our estimates of current fishing mortality rates are sensitive to the assumption that $M = 0.10$ (Table 6). This is the best estimate of natural mortality derived by Sainsbury (1982).

Modeling and implications for management

Of the two reference points we use for evaluating fishing mortality rate in the *H. iris* fishery, $F_{0.1}$ is smaller than $F_{25\%}$ for both regions. This result is insensitive to the assumed M and indicates that $F_{0.1}$ management is more conservative than $F_{25\%}$ management.

The estimated current fishing mortality rates for both regions are greater than both reference levels of F; this result is also insensitive to the assumed value of M. If the underlying assumptions hold, therefore, the current fishery is more intense than can be sustained in the long term in these regions. Egg production at the estimated present level of fishing mortality is about 18% (Table 7). This is lower than prudent management would probably require.

Both reference points are sensitive to several assumptions, similar to those discussed above: random recruitment variation, constant age-independent M, constant growth rates, and the assumed value of M (reviewed by Hancock 1979, Vetter 1988, Breen 1991).

The impact of varying the minimum legal size appears small in comparison with the sensitivity of YPR and egg production analysis to M (Table 7). Neither YPR nor egg production at equilibrium would be affected much by changing the MLS, at least over the range examined. Maximizing YPR by adjusting the MLS would require a much more precise knowledge of M. YPR is robust to changes in F, but decreasing F to the reference level $F_{0.1}$ would increase equilibrium egg production; this would be true whatever combination of M and MLS is examined. This result is similar to that reported by Sluczanowski (1984, 1986) for Southern Australian abalones. He found that egg production could be increased markedly with little sacrifice in YPR in the fishery.

Because of the ease with which paua can be found in most sites, there is a temptation to assume that stocks are healthy and in no imminent danger of overfishing. However, based on our estimates of fishing mortality rates, the recent fishery may be simply removing an abundant accumulated stock at a rate greater than annual production in two study regions.

Our best estimates of fishing mortality rates are higher than the standard reference levels, indicating that fishing pressure should be reduced in these regions. Under an ITQ management regime, this can be addressed by reducing quotas in a QMA. Translating reductions in fishing mortality to reductions in TACCs for Quota Management Areas can be done by evaluating the Baranov catch equations (Ricker 1975). Another approach is to estimate maximum constant yields from historical catch data (Schiel 1989).

Acknowledgments

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Experimental Analysis of Habitat Quality for Juvenile Queen Conch in Seagrass Meadows

Allan W. Stoner
Veronique J. Sandt

Caribbean Marine Research Center
805 46th Place East, Vero Beach, Florida 32963

Abstract.–Transplants of juvenile queen conch *Strombus gigas* L. were conducted in the southern Exuma Cays, Bahamas, to test the relationship between large-scale patterns of distribution and differential habitat quality (as indicated by conch mortality and growth). One-year-old conch (mean shell length 93 mm) were transplanted to two locations within known conch nursery habitats, one with low and one with moderate seagrass biomass. Transplants were also made to six sites without resident conch: two sites similar to the moderate biomass site, two sites similar to the low biomass site, one site with heavy seagrass, and one on bare sand.

Mortality was low at stations with natural conch populations and/or moderate seagrass biomass. Mortality was high at all other sites, and increased with time at the sand site and at one of the low biomass sites. Growth rate was high and relatively constant through the experiment at the stations with natural conch populations and at one site with moderate seagrass biomass and no resident conch (C2). Rapidly declining growth rates were found at all other sites despite depth, sediment, and macrophyte characterisitics similar to sites with resident conch. Data on standing crops of macrodetritus at the beginning and end of the experiment indicated food limitation at one site where growth was low. Until the distribution of queen conch is understood, small-scale transplanting will provide a useful tool for evaluating distributional mechanisms and a test for habitats proposed for stock enhancement.

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Seagrass meadows are important nursery habitats for many fishes and invertebrates from high to low latitudes (Thayer et al. 1975, Kikuchi and Peres 1977, Weinstein and Heck 1979, Stoner 1983, Pollard 1984, Robblee and Zieman 1984, Sogard et al. 1987). The queen conch *Strombus gigas* L. is a large gastropod mollusc (to >250 mm shell length) which uses the seagrass habitat as a nursery (Randall 1964, Weil and Laughlin 1984, Stoner and Waite 1990). Food value makes the queen conch an important commercial species throughout the Caribbean region (Brownell and Stevely 1981, Berg and Olsen 1989).

Hatchery data suggest that pelagic larvae of the queen conch spend 18 to 40 days in the water column (Brownell 1977, Davis et al. 1987, Mianmanus 1988). The larvae settle and metamorphose in the benthos and live for the first several months in places and in ways mostly unknown at this time. Juveniles are usually 35–40 mm shell length when first observed on sandy shoals and in shallow seagrass meadows (Stoner and Sandt, unpubl. data). Primary foods for juvenile stages are seagrass detritus and algae (Stoner 1989a, Stoner and Waite 1991). In seagrass beds of the Bahama, Turks, and Caicos Is., Virgin Is., Cuba, and Venezuela, juvenile queen conch densities of 1 to 2 animals/m^2 are common (Alcolado 1976, Hesse 1979, Weil and Laughlin 1984, Iversen et al. 1987, Stoner 1989a). Recent investigations in the Bahamas show that highest densities of juvenile queen conch are associated with seagrass beds of intermediate shoot density (Stoner and Waite 1990). Older juveniles move to deeper water (Weil and Laughlin 1984), and sexual maturity is attained at approximately 3.5 to 4.0 years (Randall 1964, Appeldoorn 1988).

Large seagrass habitats (hundreds of hectares) are found near Lee Stocking I., in the Exuma Cays, Bahamas. Much of this habitat appears to be appropriate for juvenile queen conch (depth, sediments, macrophyte cover); however, conch are associated with certain geographic areas within the seagrass meadows. Five discrete juvenile populations have been observed in particular localities near Lee Stocking I. from 1984 to the present (Wicklund et al. 1988, Stoner, unpubl. data).

Reported here are the results of experimental transplants designed to examine qualities of seagrass meadows which provide optimal habitat for juvenile queen conch. The following two hypotheses were tested using conch survivorship and growth as indicators of habitat quality: (1) habitat quality is directly related to seagrass biomass; and (2) Habitats with similar depth, sediments, and macrophyte biomass have equivalent qualities as nurseries for juvenile conch.

Site description

Experiments with juvenile queen conch were conducted during the summer of 1988, at eight sites in the southern Exuma Cays, Bahamas, near Lee Stocking I. (Fig. 1). These sites included two which have natural populations of queen conch juveniles, Children's Bay Cay site 1 (C1) and Neighbor Cay site 1 (N1). Site C1 had moderate turtlegrass *Thalassia testudinum* biomass, and N1 had low biomass (Fig. 2). Site N1 had lower seagrass biomass than the optimal for juvenile conch reported by Stoner and Waite (1990) but has had a persistent population of conch since at least 1986. Two sites were chosen with macrophyte, sediment, and depth characteristics similar to C1, but with no resident conch populations. Children's Bay Cay site 2 (C2) was in the same seagrass bed as C1 but 0.5 km to the southeast; the other site was west of Lee Stocking I. (L1). An additional two sites were chosen for similarity to N1: one site was north of Lee Stocking I. (L3) and the second near Windsock Cay (W1).

To examine the effects of seagrass biomass in extreme cases, two additional sites were chosen. A sand bank site, Children's Bay Cay site 3 (C3), was selected where there was no macrophyte cover but which has a regular transience of juvenile conch. One additional site, Lee Stocking I. site 2 (L2), was chosen for high seagrass and detrital biomass, 300 m northwest of L1.

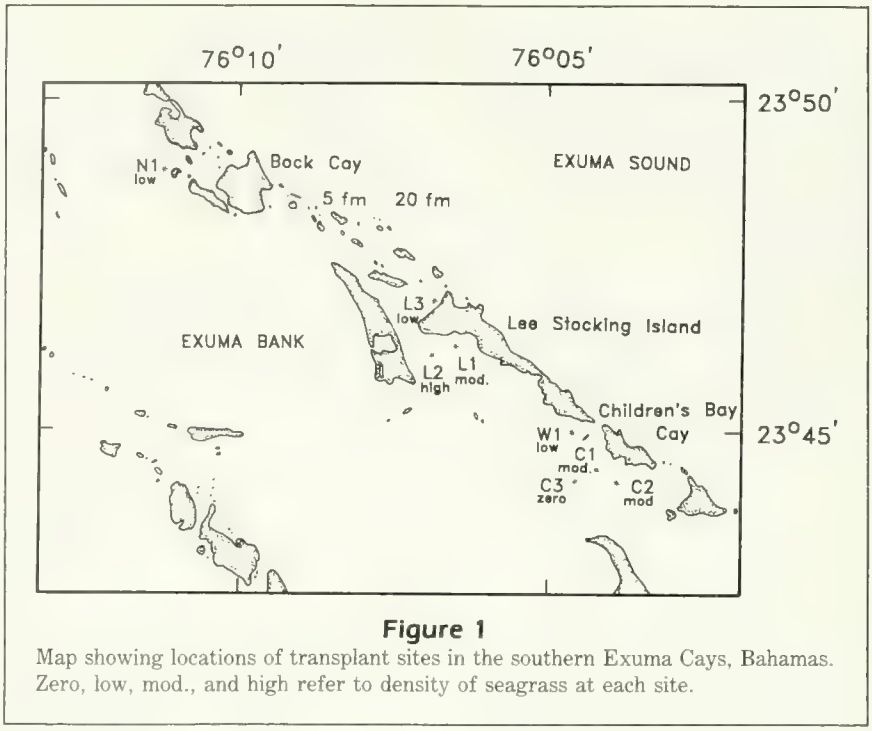

Figure 1

Map showing locations of transplant sites in the southern Exuma Cays, Bahamas. Zero, low, mod., and high refer to density of seagrass at each site.

Methods and materials

Two topless cages were constructed at the eight experimental sites with 2.0 cm black plastic mesh wired to reinforcement bar driven into the sediment. The

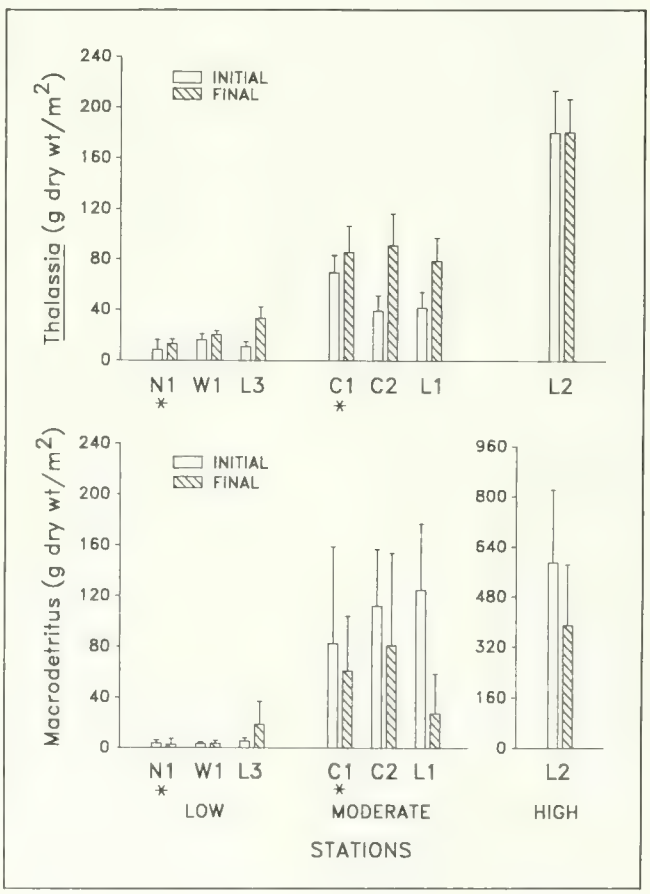

Figure 2

Standing crop of *Thalassia testudinum* and macrodetritus at sites where juvenile queen conch were transplanted. Histograms are mean values found in enclosures at the beginning and end of the experiment. Error bars are ± standard deviation. Note the change of scale for macrodetritus at station L2. Asterisks indicate stations with resident conch. Station C3 (not shown) had zero macrophyte biomass.

Table 1

Habitat characteristics of eight sites where juvenile queen conch were transplanted. Depth is the mean at low water. Values for sediments are mean ± standard deviation (n 2). Asterisks and plus signs indicate mean values which are not different statistically (ANOVA and Neuman-Keuls test; $P<0.05$).

Site	Resident conch	Seagrass biomass	Depth (m)	Sediment grain-size (ϕ)	Sediment sorting (ϕ)	Sediment organics (%)
C3	No	Zero	1.3	1.50±0.02*	0.84±0.10*	2.38±0.33+
N1	Yes	Low	2.3	1.52±0.10*	1.14±0.06*	2.68±0.14*+
L3	No	Low	2.2	2.02±0.30*	1.08±0.20*	3.66±0.33*
W1	No	Low	2.0	1.82±0.20*	1.47±0.28*	3.83±0.47*
C1	Yes	Moderate	3.6	2.56±0.29*	1.39±0.22*	3.76±0.33*
C2	No	Moderate	3.7	1.15±0.11*	1.62±0.19*	2.80±0.33*+
L1	No	Moderate	3.4	2.26±0.23*	1.40±0.23*	2.92±0.32*+
L2	No	High	3.7	2.40±0.19*	1.04±0.07*	5.36±0.48

cages were 30 cm high, 5 m in diameter, and pushed into the sediment approximately 2.0 cm to prevent loss of animals. Exact positions of the cages were chosen to provide uniformity in macrophyte cover at each site, and to insure that sites selected for similar characteristics (C1, C2, L1 and N1, L3, W1) had equivalent seagrass and detrital cover as well as sediment quality (Table 1, Fig. 2).

Previous experiments with the same cage design at Children's Bay Cay site 1 showed that the cages did not effect sediment grain-size, sediment chlorophyll, or accumulation of detritus. Enclosed animals had growth rates equivalent to individuals tagged and released in the field surrounding the enclosures (Stoner 1989a).

Animals used in this experiment were 1-year-old *Strombus gigas* collected from the sand bank near Children's Bay Cay. At the beginning of the experiment, all of the conch were between 82 and 105 mm total shell length. Mean lengths in individual treatments were not different at the beginning of the experiment (ANOVA, F 1.90, $P>0.05$), ranging from 92.0 to 94.3 mm. After measuring habitat characteristics (see below) and clearing all noticeable macroinvertebrates from the 16 enclosures, 24 individually tagged and measured conch were placed in each cage (1.2 conch/m^2), yielding a density equivalent to mean summer population density at C1 and N1. Dead or lost conch were replaced to maintain the population density within cages (Table 2). Replacements were of a size similar to the mean conch size in a particular treatment at the replacement time. Conch were marked with vinyl spaghetti tags (Floy Tag & Mfg., Inc.) tied around the shell spire.

All transplants were made by 26 April 1988, and measurements of total shell length (spire to siphonal canal) were taken with calipers at 35, 75, and 120 days. Growth rate was determined on the basis of mm shell growth per day. Each enclosure was examined at approximately 2-week intervals to determine mortality rates over time, to replace dead conch, and to remove invading invertebrates. One of the cages at C3 was destroyed by wave action in June 1988, and all of the enclosed animals were lost. This cage was rebuilt and new animals were introduced on 23 June.

At the end of the experiment, soft tissue weight of individual conch was determined by drawing the animal from its shell after freezing and subsequent thawing. Wet weight was measured after washing away feces and light blotting of the tissues. Body condition was determined by the ratio of wet weight:shell length.

Living macrophytes and macroscopic detritus were collected from each enclosure at the beginning and end of the experiment. Four replicates were taken from 25×25 cm quadrats into nylon bags (3.0 mm mesh) for determination of aboveground biomass. Individual samples were divided into green *Thalassia testudinum* blades and detritus (senescent blades and blade fragments). The only other macrophytes collected were the seagrasses *Syringodium filiforme* and *Halodule wrightii* found in very small amounts, and an occasional calcareous green alga *Rhipocephalus phoenix*. The aboveground fractions were dried at 80°C to constant weight. *Rhipocephalus phoenix* was not included in analysis of macrophytes because of the large bias created in dry weight and because the alga is not consumed by juvenile conch.

Sediments to 5 cm depth were sampled with a 3.5 cm diameter core tube, one sample per enclosure. These samples were frozen until laboratory analyses were performed. Sediment organic content was determined by drying a subsample of approximately 50 g wet

Table 2

Summary of replacements made for loss or mortality of juvenile queen conch in enclosures, by date, site, and cage number. Twenty-four animals were maintained per cage, 26 April–25 August 1988.

Site	Cage	Resident conch	Seagrass biomass	11 May	31 May	21 June	11 July	1 August	Total
C3	1	No	Zero	1	2	5	1	Terminated	9
	2	No	Zero	1	0	5	4	Terminated	10
N1	1	Yes	Low	0	0	0	0	0	0
	2	Yes	Low	0	0	0	0	0	0
L3	1	No	Low	4	2	11	3	11	31
	2	No	Low	1	9	3	4	1	18
W1	1	No	Low	0	0	1	0	0	1
	2	No	Low	0	0	3	8	20	31
C1	1	Yes	Moderate	0	0	0	0	0	0
	2	Yes	Moderate	0	0	0	0	0	0
C2	1	No	Moderate	1	0	2	0	1	4
	2*	No	Moderate	1	3	1	0	0	5
L1	1	No	Moderate	0	4	4	0	2	10
	2	No	Moderate	2	4	0	0	2	8
L2	1	No	High	6	7	9	3	1	26
	2	No	High	2	4	5	6	4	21

*This cage was rebuilt and all animals were replaced on 23 June 1988.

weight at 80°C to constant weight and incineration at 500°C for 4 hours. Organic content was quantified as the percent difference between dry weight and ash-free dry weight. Another subsample of approximately 50g was analyzed for granulometric properties. The sample was washed to remove salts and to extract the silt-clay fraction (<62μm) which was analyzed with standard pipette procedures (Galehouse 1971). The sand fraction (>62μm) was analyzed with standard sieve fractionation procedures (Folk 1966). Product-moment statistics were generated for mean grain-size and sortedness (McBride 1971).

Analysis-of-variance techniques were applied according to Sokal and Rohlf (1969), with $\log_{10}$ transformations where Bartlett's test indicated heterogeneity of variances (macrophyte data). Conch growth data proved to be heterogeneous in variance in most cases, as indicated by Bartlett's test and plots of means versus variances. Heterogeneity was improved little by log-transformation. Additionally, necessary replacement of conch during the transplant experiment produced a violation in independence in the growth data. For these reasons, Kruskal-Wallis analysis of variance was followed by nonparametric Mann-Whitney U-tests for multiple comparison of growth rates.

Results

Changes in habitat characteristics

Juvenile conch were transplanted to four different habitat types based upon macrophyte biomass: zero, low-, moderate-, and high-biomass habitats (Table 1). Sediment grain-size varied from 1.15 to 2.56 ϕ at the eight sites; however, there were no significant differences in mean values (ANOVA, F 2.26, $P>0.05$), and all are classified as fine to medium sand. Similarly, there were no differences in sediment sorting coefficients (F 2.09, $P>0.05$), with all sites except the bare sand (C3) in the poorly sorted range. Significant differences occurred in sediment organic content (F 15.97, $P<0.001$) with highest values at the high-biomass site (L2) and lowest at the sand site (Table 1). There were no significant differences in sediment organics among the sites with low or moderate biomass.

At the beginning of the experiment there were no significant differences in biomass of either seagrass or macrodetritus between the two cages at any site (Student's t-test, $P>0.05$). Analysis of variance indicated that macrodetritus varied significantly (F 76.48, $P<0.001$) among the eight sites, but there were no significant differences in mean values for the three low-biomass stations (N1, L3, W1) or for the three moderate biomass sites (C1, C2, L1) (Neuman-Keuls test, $P>0.05$). Macrodetritus was more abundant at the

high-biomass site (L2) than at any other site ($P<0.05$), and zero at the sand site (C3) (Fig. 2). The same pattern occurred with living seagrass biomass, except that site C1 had significantly higher biomass than the other moderate-biomass sites, but less than that found at the high-biomass location (L2) (ANOVA, F 58.12, $P<0.001$; Neuman-Keuls test, $P<0.05$).

For analysis of seagrass and macrodetritus standing crops at the beginning and end of the experiment, paired-comparison analysis of variance was conducted, where differences between cages and the effect of time were examined. Significant difference between cages occurred only at N1 where enclosure 2 had a higher biomass of living seagrass than enclosure 1 (F 7.46, $P<0.05$). Paired cages had similar amounts of macrodetritus at all sites ($P>0.05$). Significant differences with time were found at L1 where detritus decreased (F 13.22, $P<0.005$), while living seagrass increased with time (F 20.15, $P<0.001$). Seagrass increased also at C2 (F 23.12, $P<0.001$) and at L3 (F 34.89, $P<0.001$). No other significant time effects occurred for either macrodetritus or seagrass biomass.

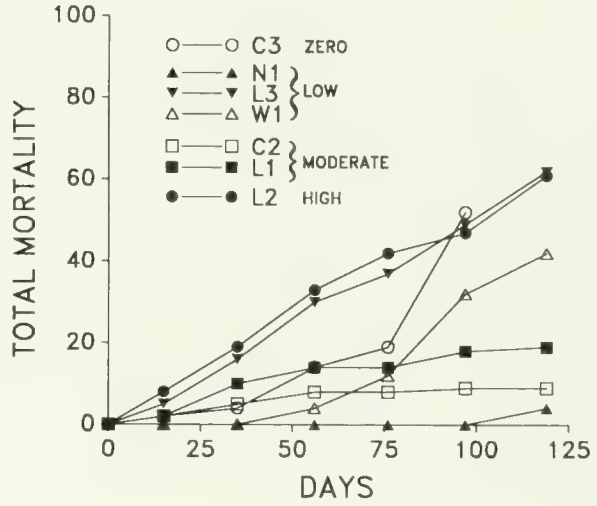

Figure 3
Total mortality of juvenile queen conch shown as a function of time at eight transplant sites near Lee Stocking I. Values are direct counts where 48 conch were transplanted to each site at the beginning of the experiment and replaced upon death. There was zero mortality at station C1 (not shown). Conch were resident at stations C1 and N1.

Mortality

Mortality at experimental sites with natural populations of conch was low, ranging from zero at site C1 to a total of only four individuals during the last three weeks of the experiment at site N1 (Fig. 3). Total mortality at the sites with moderate seagrass density and no resident conch was also low: nine individuals at station C2 and 19 at L1. At both of these sites, mortality rates decreased with time. Mortality was high at all other sites, with either a constant (sites L2 and L3) or accelerating rate (C3 and W1). By the end of the experiment, 61 animals had died at the high-biomass site (L2) and 61 had died at one of the low-biomass sites (L3). At the sand site (C3), the transplant experiment was terminated after 95 days because of rapidly accelerating mortality.

Kruskal-Wallis test was insufficiently powerful to distinguish mortality differences among the sites ($H_{adj.}$ 13.37, P 0.064) despite mortality rates ranging from 0 to 129% of the original number of conch transplanted. This is related to the low number of degrees of freedom in the design (2).

Growth

Growth rates decreased over the three experimental periods at most of the stations, but the decrease was variable among stations, and most extreme at W1 (Fig. 4). Because of station-time interaction in growth rates, Kruskal-Wallis analyses were performed for each growth period to test for station effects. In all cases the effect of site was highly significant ($H_{adj.}$ 164, $P<0.001$ for period 1; $H_{adj.}$ 234, $P<0.001$ for period 2; and $H_{adj.}$ 209, $P<0.001$ for period 3).

During the first growth period, there were no significant differences between growth rates at low-biomass site W1 and moderate biomass site C2 (Mann-Whitney U-test, U 993, P 0.441), between moderate-biomass sites C1 and L1 (U 858, P 0.297), or between sites N1 and L2 (U 825, P 0.572). Growth rates at W1 and C2 were higher than all other sites ($P<0.05$). Rates at sites L3 and C3 were different from all other sites ($P<0.05$). During this period there were no significant differences in growth rates between paired cages ($P>0.05$).

During period 2, growth rates at C1, C2, and N1 were higher than those at the five other stations ($P<0.05$) and different from one another ($P<0.05$). Despite negative growth (shell erosion) at L2 and L3, growth rates at L2, L3, C3, and W1 were not different ($P>0.05$). A significant difference in growth rates between cages at C3 (U 371, P 0.001) was the result of new animals being introduced in the rebuilt cage 1 during this period; however, growth rates were low in both cages.

As in period 2, highest growth rate during period 3 was observed at the moderate-biomass site C2 where there was no resident conch population. Rates at W1,

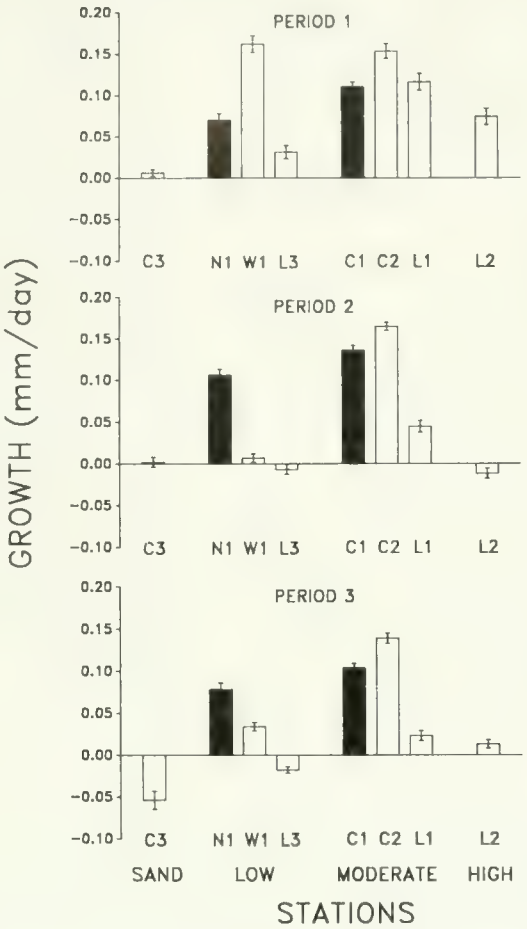

Figure 4

Growth rates for juvenile queen conch at eight transplant sites during three growth periods. Values are mean ± standard deviation. Black bars represent growth rates at sites with resident conch populations. Period 1 = 35 days, Period 2 = 40 days, Period 3 = 45 days.

Table 3

Condition factor of juvenile queen conch transplanted to eight different sites. Values are mean ± standard deviation (n 15). Vertical bars indicate sites for which medians were not different (Mann-Whitney U-tests, $P>0.05$).

Site	Resident conch	Seagrass biomass	Condition factor
C2	No	Moderate	0.257 ± 0.030
C1	Yes	Moderate	0.246 ± 0.031
N1	Yes	Low	0.227 ± 0.031
L2	No	High	0.216 ± 0.036
L1	No	Moderate	0.208 ± 0.025
L3	No	Low	0.188 ± 0.034
W1	No	Low	0.180 ± 0.030
C3	No	Zero	0.165 ± 0.020

L1, and L2 were low and not different $P>0.05$). Growth rates at all other sites were different, and strongly negative growth rates occurred at station C3 and L3. There were no significant cage differences at any of the sites during this period ($P>0.05$).

High growth rates at sites C2 and C1 were associated with high body condition (Table 3). Predictably, condition was low in the bare-sand habitat and other sites where survivorship was low (e.g., L3, W1), and there were various site differences (Kruskal-Wallis test, $H_{adj.}$ 57.38, $P<0.001$) (Table 3). Despite high mortality and low growth rate at the high-biomass site (L2), condition factor at that site was not significantly different from site N1, a natural conch habitat.

Comparing rates of mortality and growth, a pattern emerges: low growth occurred with high mortality at sites C3 and L2. Accelerating mortality and rapidly declining growth rates were found at W1 and L3, while mortality remained low and growth rates high at C1, C2, and N1. At L1, mortality was low but growth declined from a high rate in the first period.

Discussion

Growth rates found in the natural conch habitats (C1 and N1), between 0.1 and 0.2 mm/day, were similar to those determined for free-ranging juveniles at C1 during summer 1985 (0.12 mm/day)(Wicklund et al. 1988), and summer 1987 (0.10–0.15 mm/day)(Stoner 1989a). The rates reported here are also similar to those reported from Los Roques, Venezuela, where growth curves give mean growth rates of 0.16 mm/day for tagged conch between 85 and 105 mm in shell length (Laughlin and Weil 1982), and 0.14 mm/day for 90 mm conch (Brownell 1977). These results suggest that enclosures used in this experiment did not inhibit growth in the test animals.

So that the numbers of conch in the enclosures remained constant, dead conch were replaced with new individuals which, in the less optimal sites, grew at a rate slightly higher than conch enclosed earlier. Replacement, therefore, results in overestimation of growth rate (and probably survivorship) in the poor-quality habitats and conservative separation of sites. Differences in shell length among the experimental sites by the second and third growth periods, and slight differences in growth rates of conch between 90 and 120 mm (Brownell 1977) would have only a minor in-

fluence on site differences. Despite these limitations, high mortality rates and low or negative growth rates provide clear evidence that five of the sites without resident conch (except site C2) were poor habitats for juvenile queen conch.

Stoner and Waite (1990) showed that 1- and 2-year-old conch actively select areas with intermediate seagrass biomass over areas with high and low biomass. Additionally, it was shown that seagrass shoot density and biomass were good predictors of juvenile conch distribution within nursery habitats. Among the sites which were known to serve as natural habitats for queen conch (C1, C3, N1) there was a direct relationship between seagrass biomass and habitat quality, as measured by conch growth. On the larger scale of this study, however, seagrass density was not a good predictor for conch success, and other variables—probably trophic factors—need to be examined.

Adult and subadult queen conch are generally considered to be herbivores (Robertson 1961, Randall 1964, Hesse 1976), but recent data on juvenile conch living in seagrass beds show that seagrass detritus is consumed in large quantities, and macroalgae such as *Batophora oerstedi* and *Laurencia poitei* are primary sources of nutrition (Stoner and Waite 1991). Field experiments have shown that juvenile conch can have a major influence on detritus and other characteristics of the benthic environment, with much of the benthic productivity being removed by grazing (Stoner 1989a, b). The observed depletion of detrital biomass followed by decreasing conch growth rates at the moderate biomass site L1 suggests trophic limitation at that station.

Abundance of macrophytes does not necessarily provide superior habitat. Site L2 had a thick accumulation of detritus and high seagrass biomass, but conch transplanted to that site had high mortality and low growth rates. Randall (1964) noted that young conch may not be able to move readily through dense seagrass stands, and are rarely found in that habitat type.

No attempt is made here to equate mortality rates in the transplants with natural mortality because of potential density-dependent effects on predation rate, partial exclusion of predators by cages, and uncertainty in the sources of mortality. Observations of potential queen conch predators in the enclosures were rare. The tulip snail *Fasciolaria tulipa* was seen attacking conch three different times, and in a few instances the giant hermit crab *Petrochirus diogenes* was found in empty shells; both of these species are known predators on queen conch (Randall 1964, Jory 1982). The apple murex *Murex pomum* and hermit crabs *Paguristes* sp. were observed occasionally in the enclosures, but both are thought to be scavengers (Jory and Iversen 1983, Iversen et al. 1986). Lack of broken shells, low body condition, and low shell growth rates lead us to conclude that much of the mortality in "poor" habitats was a result of inadequate food resources. On the other hand, large differences in mortality rate between the two enclosures at two of the sites suggest that heavy predation may have occurred in some cages.

The fact that one site with no resident juvenile conch (C2) produced high growth rates and survivorship suggests that queen conch do not occupy all suitable habitats. Several explanations are plausible: Pelagic larvae may not be dispersed to the area, settlement may not occur, or early-juvenile stages may suffer high mortality rates at the site. It is also possible that, historically, site C2 has been a nursery site for queen conch. Macroscopic conch shell fragments at the site were found in a density of 3.0 fragments/m^2; this is lower than the density at site C1 (6.8/m^2), but considerably higher than that in other non-conch areas (e.g., density at L1 was 0.05 fragments/m^2) (Stoner and Yoshioka, unpubl. data).

Presence or absence of juvenile queen conch in seagrass meadows appears to be mediated by site-specific characteristics. Habitat quality, as measured by growth rate, was related directly to seagrass biomass in natural conch sites; however, the hypothesis that habitats with similar depth, sediments, and macrophyte biomass have equivalent qualities as nurseries for juvenile conch is clearly rejected. Until the distributional ecology of queen conch is understood, small-scale transplanting will be a valuable tool in manipulations designed to test the significance of other environmental variables, and as a means of testing habitats where enhancement of stocks is proposed.

Acknowledgments

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Otolith Size versus Weight and Body-Length Relationships for Eleven Fish Species of Baja California, Mexico

David Aurioles Gamboa

Departamento de Recursos Marinos, Division de Biologia Marina
Centro de Investigaciones Biologicas de Baja California Sur
Apartado Postal 128, La Paz, Baja California Sur, Mexico

Identification of otoliths recovered from scats or stomachs of marine mammals has been used in feeding-habit studies in recent years (Fitch and Brownell 1968, Brown and Mate 1982, Antonelis et al. 1984, Aurioles et al. 1984). Because of the relatively large number of pinniped scats available, this method has proven useful for identifying prey. However, the method depends on the laborious collection of otoliths from fish in the study area. The relative frequency of a prey species in the diet is determined by the number of otoliths (either right or left) counted. However, two prey species with the same otolith count may not be of equal importance in the diet because of differences in biomass. Antonelis et al. (1984) addressed this problem by estimating the biomass of fish and one species of squid off California, from regressions of weight (biomass) versus the size of otoliths (or squid beaks). The relationship of otolith length to fish size or weight has been reported for other areas (Frost and Lowry 1981, Wyllie Echeverria 1987).

Eleven known species of California sea lion *Zalophus californianus* prey (Aurioles et al. 1984, Lowry and Oliver 1986) were sampled to obtain weight, body length, and otolith length to estimate regressions. These results will be useful for estimating prey size and weight in feeding-habit studies in areas where these fish species occur.

Methods

Fish were sampled by bottom trawling with commercial shrimp nets. Trawls were conducted at depths of 30–200 m on the continental shelf off the Pacific coast of Baja California (23°–27°N lat.) and in the southern Gulf of California. Trawling, fish sampling, and fish measurements were conducted aboard the Research Vessel El Puma owned by the Universidad Nacional Autonoma de Mexico during cruises in the summer and fall of 1987 and the summer of 1988.

Standard length (mm) and weight (g) were recorded for fresh fish specimens. Weight (±0.01 g) was measured using a digital scale (Ohaus). Calipers were used to measure the greatest length (anterior tip to posterior projection) of each dissected sagittal otolith. Values were averaged for each otolith pair. Linear regressions were used to determine the relationship between standard length or fish weight and otolith length.

Results and discussion

Eleven fish species were studied (Table 1). Serrano *Serranus aequidens* and yellowbelly lizardfish *Synodus jenkinsi* were collected in Bahia de La Paz (Golfo de California), while the remaining nine species were typically found off the western coast of Baja California.

The standard length of fishes sampled in this study fell within lengths reported in the literature (Miller and Lea 1976, Eschmeyer et al. 1983) (Table 1). Linear regression of otolith length (mm) against fish length for all species are given in Table 2.

A high correlation coefficient was obtained for the longfin sanddab *Citharichthys xanthostigma* (r 0.974) in spite of the small sample size (Table 2). This was probably due to the relatively large size range of individuals in the sample. Scatter plots of fish length on otolith length for 8 of the 11 species are shown in Figures 1–8. The remaining three species had correlation coefficients smaller than r 0.86 and were not plotted.

The equation for hake (Table 2) was the highest for the sampled species. Antonelis et al. (1984) calculated a regression equation for Pacific hake *Merluccius productus* collected off California. Using an otolith of 6 mm in length in their equation ($Y = 26.2 + 19.38x$), the predicted fish length would be 142.5 mm. Using the equation in Table 2 for hake collected in this study yields a length of 113.76 mm. A "dwarf" Pacific hake in Baja California waters was reported by Vrooman and Paloma (1977). Inada (1981) in an extensive study of the genus stated that the "dwarf" form is actually Panama hake *Merluccius angustimanus*. It is probable that our sample specimens were this species, which is limited in range to the area between 24° and 27°N latitude. According to Vrooman and Paloma (1977), and confirmed by several cruises conducted by the Centro de Investigaciones Biologicas de B.C.S (CIB), the southern limit of distribution of the "large" form of Pacific hake is probably near Bahia Sebastian Vizcaino (28°N lat.).

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Table 1

Lengths and weights of fish collected off Baja California that are known prey of the California sea lion *Zalophus californianus*.

Scientific name	Common name*	Maximum standard length (mm)**	n	Ranges of lengths and weights (mm)	(g)
Hippoglossina stomata	Bigmouth sole	400	83	95–230	11.8–240
Lepophidium prorates	Pink cusk eel	–	39	107–223	3.6–62
Ophidion scrippsae	Basketweave cusk eel	280	106	160–242	37.8–115
Serranus aequidens	Serrano	–	43	89–166	13.3–88.5
Prionotus stephanophrys	Lumptail searobin	390	193	67–240	5.6–263
Merluccius angustimanus	Panama hake	910	183	89–220	5.4–103.6
Calamus brachysomus	Pacific porgy	610	36	163–350	141.3–1135.6
Citharichthys xanthostigma	Longfin sanddab	250	46	59–200	1.8–161
Porichthys myriaster	Specklefin midshipman	510	75	140–350	25.7–527.5
Synodus lucioceps	California lizardfish	640	34	160–430	29.4–578
Synodus jenkinsi	Yellowbelly lizardfish	–	41	185–406	46.5–580.2

*Common name assigned in this study.
**Data from Miller and Lea 1976, Eschmeyer et al. 1983.

Table 2

Regression equations for fish length (Y) vs. otolith length (X) for fish collected off Baja California that are known prey of the California sea lion *Zalophus californianus*.

Species	n	Equation* $Y = a + bX$	Correlation coefficient	Percent r^2
Bigmouth sole	83	$Y = (-5.976) + 5.47X$	0.873	76.26
Pink cusk eel	39	$Y = (-3.103) + 23.76X$	0.915	83.77
Basketweave cusk eel	106	$Y = (3.408) + 29.30X$	0.930	87.86
Serrano	43	$Y = (1.539) + 1.830X$	0.857	73.56
Lumptail searobin	193	$Y = (-17.649) + 27.26X$	0.928	86.22
Panama hake	183	$Y = (13.564) + 16.7X$	0.979	95.89
Pacific porgy	36	$Y = (-10.337) + 4.174X$	0.945	89.31
Longfin sanddab	46	$Y = (-3.898) + 31.48X$	0.974	94.97
Specklefin midshipman	75	$Y = (-4.518) + 2.92X$	0.954	91.05
California lizardfish	34	$Y = (1.694) + 4.975X$	0.821	67.44
Yellowbelly lizardfish	41	$Y = (-2.515) + 5.827X$	0.864	74.78

*$P = 0.01$ for all equations.

Since equations for both the California and the Baja California samples were highly significant, the observed differences cannot be explained by measurement errors or data variation, but probably reflect different hake species.

Fish weight was regressed against otolith and fish lengths (Tables 3 and 4). When otolith size was used to estimate fish weight directly, the correlation coefficient, and consequently percent r-squared for some species (Table 3), was slightly smaller than the respective values of fish weight estimated from fish length (Table 4). Regression lines and scatter plots for eight fish species studied are shown in Figures 1–8.

Coefficients of fish weight on fish length were the highest (Table 4). The value of r^2 was greater than 90% in all cases. Thus, when comparing prey importance based on biomass in feeding-habit studies, both equations (Tables 3 and 4) should be used to estimate weight.

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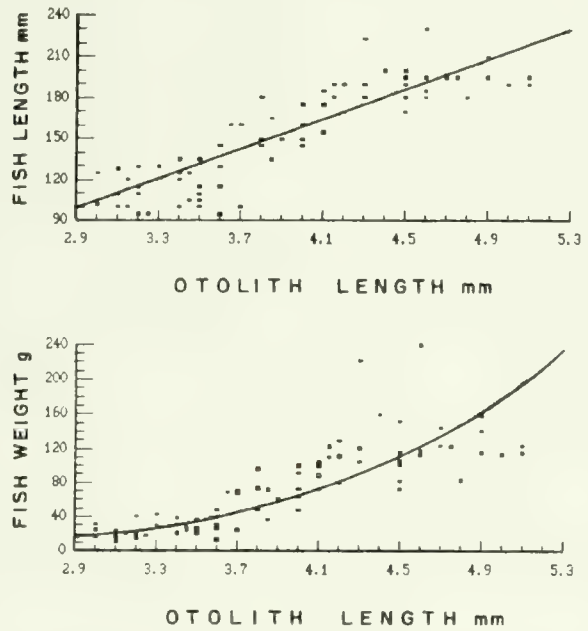

Figure 1
Relationship of fish length and weight to otolith size for bigmouth sole *Hippoglossina stomata* from Baja California.

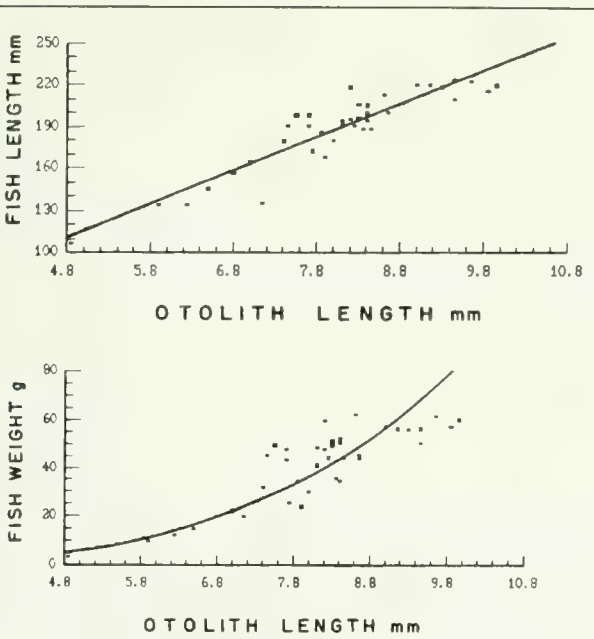

Figure 2
Relationship of fish length and weight to otolith size for pink cusk eel *Lepophidium prorates* from Baja California.

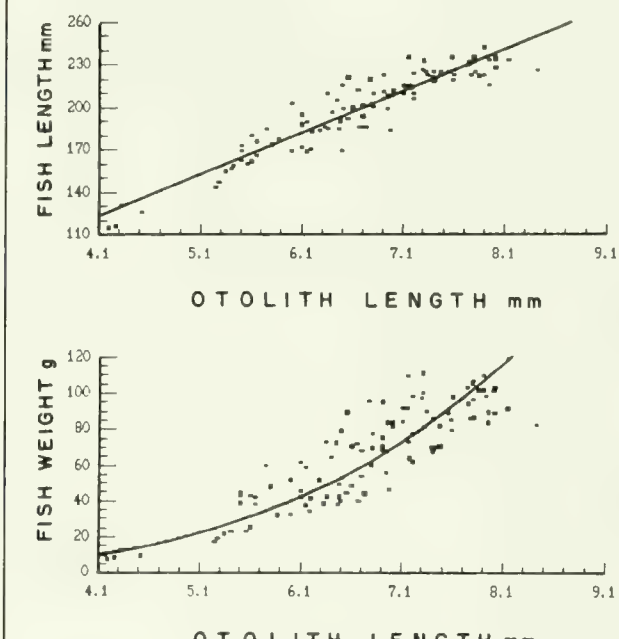

Figure 3
Relationship of fish length and weight to otolith size for basketweave cusk eel *Ophidion scrippsae* from Baja California.

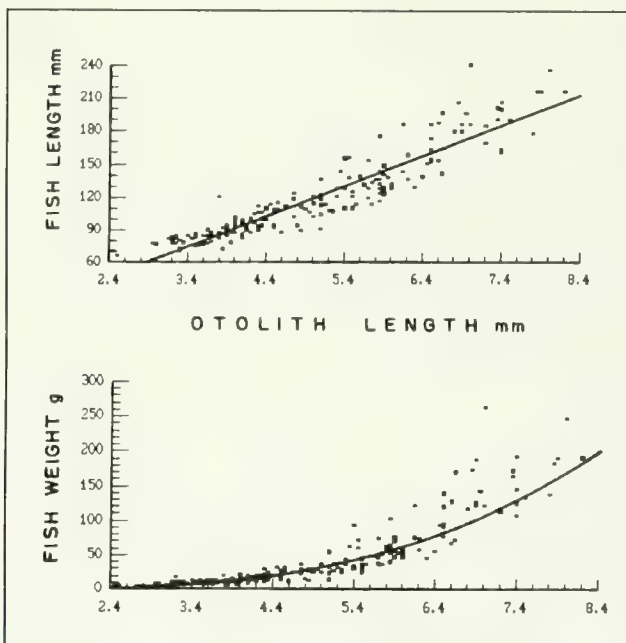

Figure 4
Relationship of fish length and weight to otolith size for lumptail searobin *Prionotus stephanophrys* from Baja California.

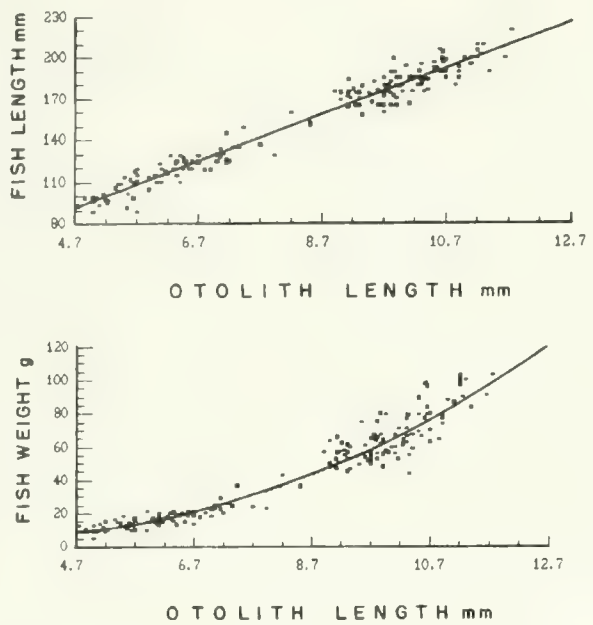

Figure 5
Relationship of fish length and weight to otolith size for Panama hake *Merluccius angustimanus* from Baja California.

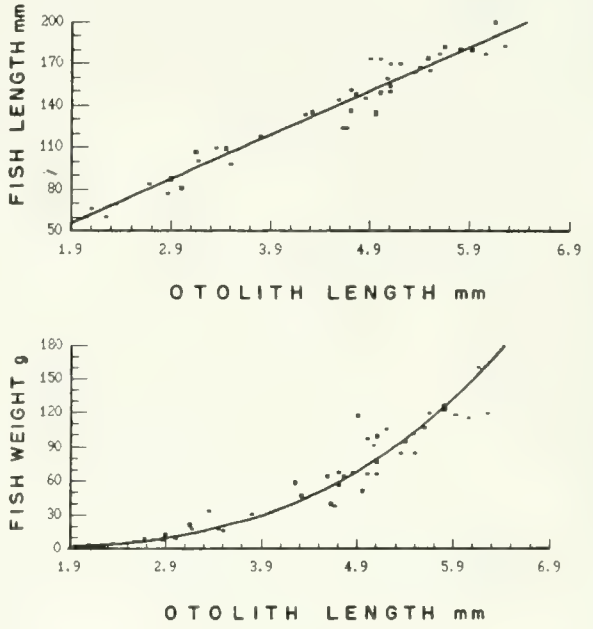

Figure 7
Relationship of fish length and weight to otolith size for longfin sanddab *Citharichthys xanthostigma* from Baja California.

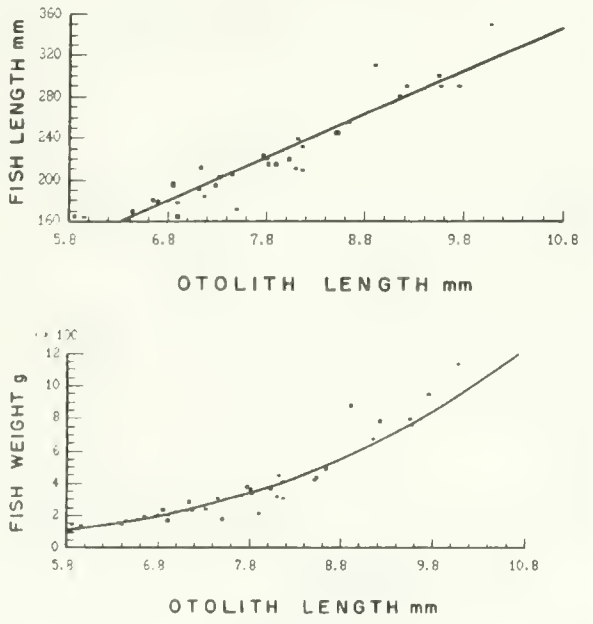

Figure 6
Relationship of fish length and weight to otolith size for Pacific porgy *Calamus brachysomus* from Baja California.

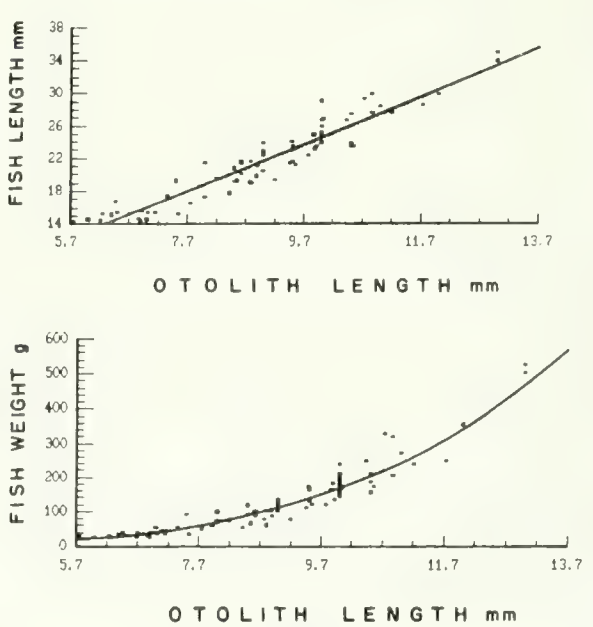

Figure 8
Relationship of fish length and weight to otolith size for specklefin midshipman *Porichthys myriaster* from Baja California.

Table 3

Regression equations for fish weight (Y) vs. otolith length (X) for fish collected off Baja California that are known prey of the California sea lion *Zalophus californianus*.

Species	Equation* $Y = a X^b$	Correlation coefficient	Percent r^2
Bigmouth sole	$Y = (-2.084) X^{4.51}$	0.877	76.93
Pink cusk eel	$Y = (-4.222) X^{3.75}$	0.912	83.20
Basketweave cusk eel	$Y = (-2.666) X^{3.54}$	0.908	82.60
Serrano	$Y = (-1.097) X^{2.63}$	0.858	73.69
Lumptail searobin	$Y = (-2.030) X^{3.44}$	0.944	89.25
Panama hake	$Y = (-2.091) X^{2.71}$	0.973	94.72
Pacific porgy	$Y = (-2.238) X^{3.0}$	0.948	89.88
Longfin sanddab	$Y = (-1.507) X^{3.6}$	0.979	95.90
Specklefin midshipman	$Y = (-3.756) X^{3.85}$	0.961	92.38
California lizardfish	$Y = (-2.65543\,E\text{-}3) X^{3.01}$	0.867	75.17
Yellowbelly lizardfish	$Y = (-0894) X^{3.69}$	0.854	73.09

* Intercept in parenthesis is equal to Log of a. $P = 0.01$ for all equations.

Table 4

Regression equations for fish weight (Y) vs. fish length (X) for fish collected off Baja California that are known prey of the California sea lion *Zalophus californianus*.

Species	Equation* $Y = a X^b$	Correlation coefficient	Percent r^2
Bigmouth sole	$Y = (-4.181) X^{3.03}$	0.978	95.68
Pink cusk eel	$Y = (-14.51) X^{3.46}$	0.968	93.86
Basketweave cusk eel	$Y = (-4.955) X^{3.05}$	0.964	93.04
Serrano	$Y = (-3.497) X^{2.82}$	0.976	95.34
Lumptail searobin	$Y = (-11.509) X^{3.15}$	0.988	97.74
Panama hake	$Y = (-11.213) X^{2.95}$	0.981	96.41
Pacific porgy	$Y = (-2.684) X^{2.75}$	0.984	97.01
Longfin sanddab	$Y = (-13.13) X^{3.46}$	0.992	98.59
Specklefin midshipman	$Y = (-5.001) X^{3.16}$	0.981	96.43
California lizardfish	$Y = (-4.953) X^{3.0}$	0.962	92.65
Yellowbelly lizardfish	$Y = (-5.801) X^{3.31}$	0.979	96.01

* Intercept in parenthesis is equal to Log of a. $P = 0.01$ for all equations.

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Responsiveness of Starved Northern Anchovy *Engraulis mordax* Larvae to Predatory Attacks by Adult Anchovy

Clelia Booman

La Jolla Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, California 92038
Present address: Zoological Laboratory, University of Bergen
Allegate 45, N-5007 Bergen, Norway

Arild Folkvord

La Jolla Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, California 92038
Present address: Department of Fisheries and Marine Biology, University of Bergen
High Technology Centre, N-5020 Bergen, Norway

John R. Hunter

La Jolla Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, California 92038

Most studies of larval mortality have been on food, feeding, and starvation, with less work done on predation and even fewer studies on the interaction between starvation and predation (Hunter 1984). Vulnerability to predation is a product of the probability of encounter between prey and predator, and prey susceptibility (Bailey and Houde 1989). Starvation could affect one or both of these components: starving larvae might be less able to avoid attacks by predators than fed ones (Rothschild et al. 1982). On the other hand, a decrease in conspicuousness of starved larvae might reduce their probability of encounter with predators (Gamble and Fuiman 1987). In addition, slow growth caused by an inadequate food supply could result in larvae remaining in the length-classes most vulnerable to predation and thereby increase larval losses (Shepherd and Cushing 1980).

In northern anchovy *Engraulis mordax* larvae, vulnerability to predation by fishes is size-specific, thus slower growth could result in greater losses (Webb 1981, Folkvord and Hunter 1986). The objective of this study was to evaluate the effect of starvation on avoidance performance of northern anchovy. We estimated the responsiveness and escape ability of 9 mm SL (standard length) anchovy to predatory attacks by adult anchovy as a function of days of starvation. We also developed histological starvation criteria which link the nutritional condition of larvae to their responsiveness to attacks by fish predators. This could allow an assessment of the interaction between predation by fishes and starvation in the sea, because the nutritional condition of sea-caught larvae could be assessed using histological criteria (O'Connell 1976 and 1980, Theilacker 1978 and 1986).

Materials and methods

Rearing and experimental design

About 4000 northern anchovy eggs produced by a captive brood stock (Leong 1971) were placed in a 100-liter black fiberglass tank maintained at 16.0–17.4°C (mean 16.2° C). Except for minor differences, larvae were reared following the procedure outlined by Hunter (1976). Larvae were reared until they reached 9 mm live standard length (about 20 days posthatch) at which time they were used in our experiments. In the experiments, 9 mm larvae were used because smaller anchovy larvae respond less frequently (<36%) to predators (Folkvord and Hunter 1986).

When larvae reached 9 mm, they were separated into two groups by transferring about half of them to another 100-liter tank containing only filtered seawater. The transferred larvae were never fed. Avoidance performance of the starved larvae was compared with that of larvae fed daily in the original tank. Initially a series of tests was conducted to estimate if the transfer of larvae affected avoidance performance. In these tests both groups were fed and one was transferred. Mortality was higher in the transferred group over the first day, but no significant difference existed between the groups thereafter in mortality or in their response to predators using the behavioral methods outlined below.

Larvae from three different rearing groups were used. In two groups, none of the starved larvae survived more than 6 days, and in one group a few survived 7 days. Considering all groups together, about 50% of the starved larvae survived 4–5 days and only 1% survived 7 days of starvation. Thus, most of the data are for larvae starved for 1–5 days. Four groups of five adult anchovy (90–107 mm SL) were used as predators. Predators were placed in the test container (a fiberglass tank 0.75 × 2.15 × 0.83 m with a glass window on one side) about 3 weeks prior to a series of experiments. Ambient seawater

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(15.1–17.8°C) flowed continuously through the tank, except during the experiments when water flow was stopped. Two household tungsten lamps above the tank provided about 2000–3000 lux at the water surface.

The experimental procedure was similar to Folkvord and Hunter (1986). Experiments were run in the morning and early in the afternoon starting about 24 hours after onset of starvation. Adult brine shrimp (*Artemia* sp.) were used to identify variation in predator feeding behavior between and during experiments. The addition of three brine shrimp or three starved anchovy larvae or three fed anchovy larvae constituted a single trial. Each experiment started with 3 *Artemia* trials followed by 15 trials repeating the sequence; fed larvae, starved larvae, and *Artemia*. The initial three brine shrimp trials insured that the feeding performance of the predators was stable, and subsequent brine shrimp trials were to check for effects of satiation (Folkvord and Hunter 1986). The brine shrimp trials were also used to test for differences in feeding performance among predator groups. No significant differences existed among the 4 predator groups in the proportion of brine shrimp eaten in 5 minutes (99% of the brine shrimp were eaten), or in the proportion of fed or starved larvae responding to attacks (logistic regressions, $P>0.40$).

A trial began when the prey were gently poured from a beaker into the test container and ended when all three prey were consumed or when 5 minutes had elapsed. During a trial, each time a prey was attacked by a predator, we recorded whether or not the prey responded to the attack, whether or not it escaped, and the time required to capture the prey. A predator attack was defined as a change in swimming speed or direction towards a prey followed by an opening of the mouth. A response to a predator was defined as a change in larval swimming speed or direction that occurred during an attack. An escape was defined as a predator attack in which the larva responded and successfully avoided the predator. A total of 345 fed and 345 starved larvae were used in the experiments, but the results are based on the number of predatory attacks and not on the total number of larvae tested. Some larvae were attacked more than once and others were not attacked at all. If a larva was attacked more than once in an experiment, each interaction was considered a separate event. When a larva was taken immediately after release or before it had moved, the interaction was not assessed. The responsiveness to attacks was assessed in 295 out of 325 attacks by predators on fed larvae and in 266 out of 323 attacks on starved larvae.

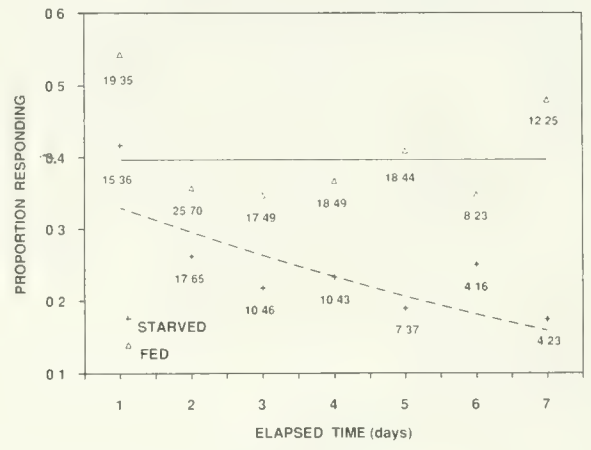

Figure 1

Proportion of fed and starved 9 mm SL northern anchovy larvae that responded to attacks of adult northern anchovy (Y), as a function of the duration of the starvation period (X = elapsed time in days). Horizontal line represents average proportion of fed larvae responding (0.4 ± 0.03); logistic regression, effect of day, $P>0.8$. Dashed line for starved larvae is given by the equation: $Y=e^{(-0.55-0.16*X)}/(1+e^{(-0.55-0.16*X)})$; logistic regression, effect of day, P 0.044. Numbers next to points are number of responses and interactions.

Assessment of nutritional condition

Histological criteria were developed to link starvation-induced changes in avoidance behavior of larvae to their nutritional condition. Samples of starved and fed larvae from each of the three groups were taken for histological analysis. Twenty starved and 10 fed larvae were collected every morning starting about 24 hours after onset of starvation. Larvae were fixed in Bouin's solution, embedded in Paraplast-plus, serially sectioned at 5 μm, and stained with Harris hematoxylin eosin-phloxin B.

O'Connell (1976) found that pancreas condition, notochord shrinkage and muscle fiber separation were the histological characteristics that best distinguished starving anchovy larvae from healthy ones during the first feeding stage (4 mm SL, about 4 days posthatch). These characteristics did not prove to be useful for the diagnosis of starvation in the 9 mm (20 day posthatch) larvae. For example, fibers of the trunk musculature were perfectly arrayed in starved 9 mm larvae, and no interfiber spaces existed in any of the larvae analyzed even after 6 days of starvation. We also found no correlation between the condition of the notochord and starvation. Also presence, size, and abundance of hindgut vacuoles were interpreted as indicators of recent feeding and not of larval condition.

The histological condition of the liver proved to be the best character for diagnosis of starvation in 9 mm larvae. Liver condition has been used for the diagnosis of starvation in fishes in combination with other characters by O'Connell (1976), Theilacker (1978), and Watanabe (1985), and liver alone was used by Storch and Juario (1983) and Storch et al. (1984). In the results section, we relate histological condition of the liver to days of starvation and responsiveness to predatory attacks.

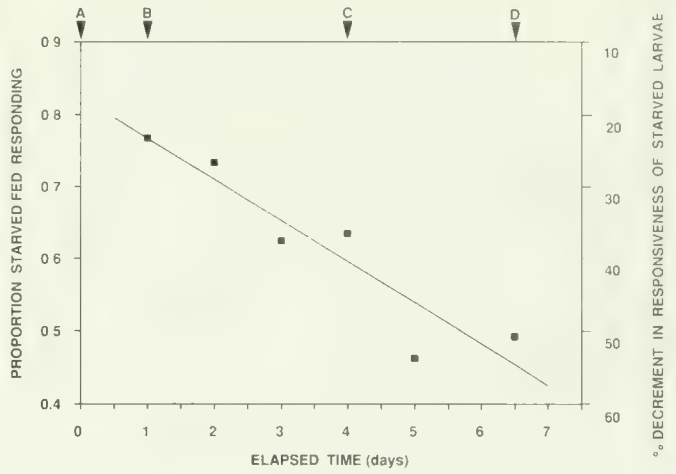

Figure 2

Responsiveness to anchovy predators of starved northern anchovy larvae (relative to fed larvae tested in the same experiment) shown in relation to duration of the starvation period and the condition of larval hepatic tissue. Data from days 6 and 7 were combined to obtain sufficiently high numbers of starved larvae. Equation for the line is $Y = 0.824 - 0.057X$ (R^2 0.87, SE est. 0.05). Histological characteristics of the liver of starved larvae are indicated with letters and arrows. (A) Glycogen vacuoles in hepatocytes, (B) no glycogen, structures unaltered, (C) hepatocytes membranes damaged, dark nuclei, and (D) cell atrophy, nuclei pycnotic and irregular.

Results

Response and escape probabilities

The proportion of larvae responding to attacks of adult anchovy progressively decreased with starvation. Forty percent of fed larvae responded to the attacks of predators, about the same proportion determined for 8.5 mm anchovy by Folkvord and Hunter (1986, test of binomial proportions, P 0.64). After 4 days of starvation 23% responded, and by 7 days of starvation 17% responded (Fig. 1). The higher value for both fed and starved larvae on day 1 could partly be due to the predator inexperience in preying on anchovy larvae, since during the acclimation period the predators had been fed only live adult *Artemia*.

Considerable variability existed in the percentage of larvae that responded to predators in the fed groups from day to day (range of daily averages 35–54%) and among predator and prey groups (range of group averages 36–45%). Since a series of trials using fed larvae always accompanied those with starved larvae, it was possible to adjust for this interexperiment variability by dividing the fraction of starved larvae that responded by the fraction of fed larvae that responded during the same experiment. After one day of starvation (that is, 24–30 hours after transfer) this ratio was 0.77, indicating that the response probability for larvae deprived of food for 1 day was 23% lower than that of fed larvae. The regression for these calculated ratios indicates that larvae starved for 4 days were 40% less likely to respond than fed larvae, and those starved for 7 days were 58% less likely to respond (Fig. 2).

Very few larvae escaped predators regardless of their nutritional state. Thus, it was not possible to evaluate the proportions escaping as a function of the duration of starvation. Considering all data combined, starved larvae were less successful in escaping predators (0.8% vs. 3.4% fed larvae; test of binomial proportions, P 0.027). Escape probabilities were lower in fed larvae in this study (3.4%) than in Folkvord and Hunter (1986, 12%) for 8.5 mm larvae (test of binomial proportions, P 0.01). Some obvious differences existed between the studies. In the present study, body size of the anchovy predators was about 10% longer, temperature in the experimental tank about 5°C lower, and the test tank acclimation period of predator groups was longer. Any of these factors could affect the probability of escape.

Relation between prey responsiveness and histological condition

Larvae deprived of food for 1 day had no vacuoles in their liver, but cellular structures showed no alterations (Fig. 3). The vacuoles seen in fed larvae presumably contain glycogen (O'Connell and Paloma 1981). Disappearance of vacuoles after 24 hours of food deprivation has also been observed by Watanabe (1985) in freshwater gobiid larvae reared at 15–20°C. At this stage of starvation, anchovy larvae were 23% less responsive to predators than were fed larvae. After 4 days of starvation, the hepatic tissue began to deteriorate; cell outlines were hardly distinguishable, and the nuclei stained darkly. Larvae with these characteristics were about 40% less responsive than were fed larvae.

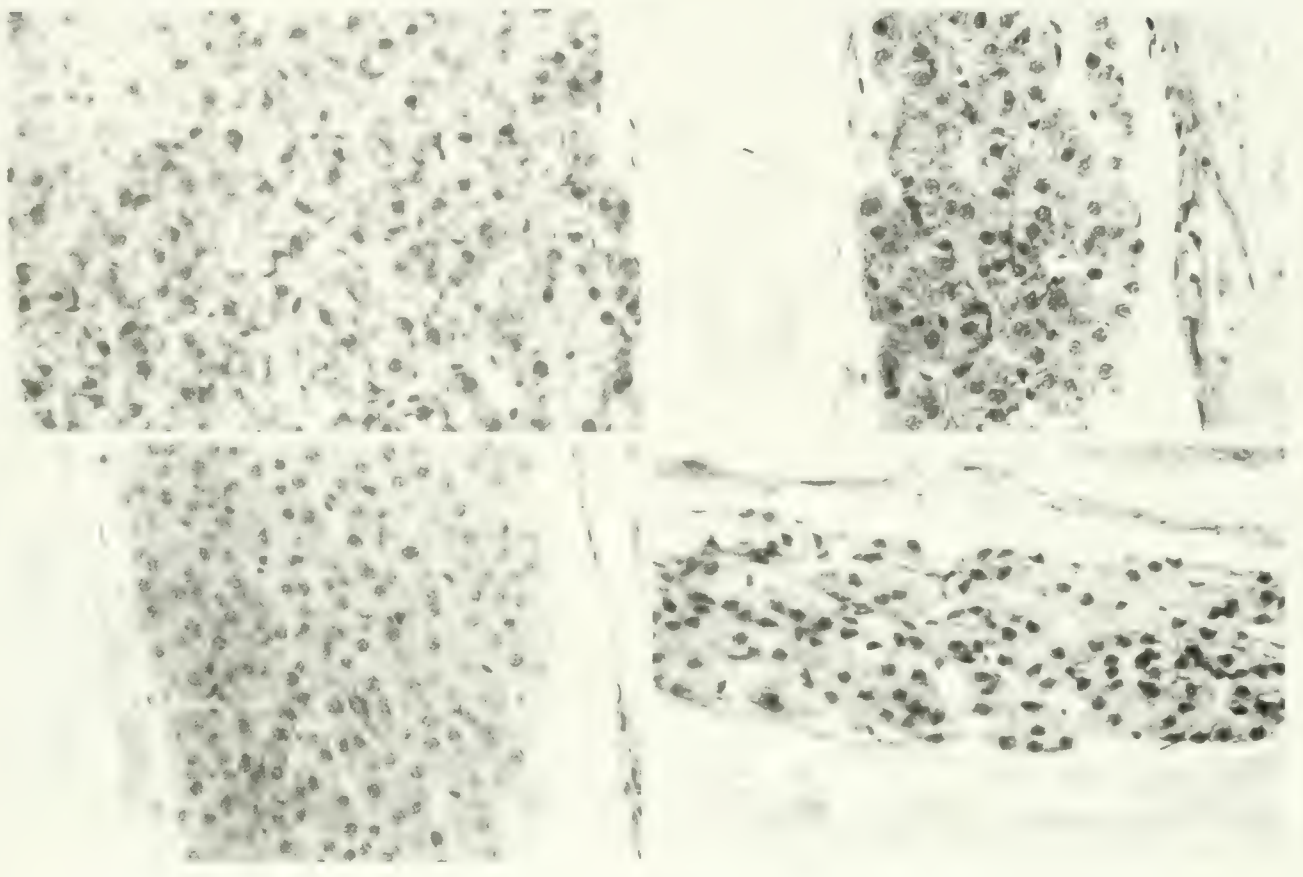

Figure 3

Condition of the hepatic tissue of larval northern anchovy after 0, 1, 4, and 6 days of starvation (white bar = 0.01 mm). (Upper left) fed larvae. White vacuolated areas may be glycogen deposits. (Upper right) 1 day of starvation. No vacuolated areas and no cellular deterioration. (Lower left) 4 days of starvation. Damaged membranes and dark nuclei. (Lower right) 6 days starvation. Hepatocytes atrophied, nuclei shrunken and pycnotic.

Hepatocytes of larvae starved for 6–7 days had atrophied, making the nuclei appear to be more densely distributed. Nuclei were pycnotic and irregular in shape. Such larvae were about 55% less responsive to predators than fed larvae.

Discussion

Starvation may affect responsiveness of larger anchovy larvae in a fashion similar to the one here described for 9 mm larvae. Preliminary measurements by Folkvord (1985) indicated that newly metamorphosed juvenile anchovy (35 mm SL) were less likely to respond if deprived of food. When deprived of food for 5 days, only 50% of the fish responded to predatory attack whereas 100% of fed fish did so. Håkanson (1989) analyzed the lipid contents of fed and starved anchovy larvae of similar age and reared at similar temperatures as in this study. He found a decrease in the content of triacylglycerol, an energy storage component, after 3 days of starvation. On the other hand, we found that the glycogen reserve in the liver was nearly depleted after one day of starvation. Lipid reserves greatly increase after metamorphosis (J.R. Hunter, unpubl. data) and consequently such a decrement in avoidance behavior with a few days of food deprivation may be limited to the larval and early juvenile period. Yin and Blaxter (1987) also determined a decrease in the response rates of unfed yolksac herring, cod and flounder larvae to tactile stimuli, especially after the point of no return (PNR). These authors determined a similar effect in the response rate of older Clyde herring larvae (36 days, 14 mm) to contact with a pipette after the PNR (6 days of starvation at 9–10 °C). A starvation-induced decrease in vulnerability to

predation because of a decrease in encounter rates between predators and prey (Gamble and Fuiman 1987) is not supported by our data. A decrease in encounter rates does not seem to have occurred, since attack rates on fed and starved larvae were the same. A change in larval activity may, however, have a greater effect on prey visibility among smaller larvae than larger ones.

Our scale of nutritional condition based on liver characteristics could be used to assess the extent of the interaction between starvation and predation in the sea. The level of cell deterioration found in larvae starved 4 days or more at 16°C most likely represents the PNR, and the starvation-induced vulnerability to predation could amplify the losses caused by starvation only up to this point. A sharp decline in cholesterol and polar lipid content was found in larval anchovy after 5 days of starvation at 15.5°C (Håkanson 1989). These lipids are cell membrane constituents. The high vulnerability of larvae starved for periods longer than 4–5 days seems of less ecological consequence, since nearly all such severely emaciated larvae would probably ultimately die of starvation. However, the increase in vulnerability over the entire starvation period is of interest, because it may affect estimates of starvation rates in the sea and possibly estimates of natural larval mortality. Clearly, rates of starvation based on daily incidence of starvation classes (Theilacker 1986) may underestimate the actual losses if starvation results in an increase in the vulnerability to predators. In addition, our results may support the hypothesis of Isaacs (1964) that daytime plankton samplers may be selective for weaker and less-responsive larvae. Such a hypothesis requires vision to be the primary sensory modality for the larval avoidance response. If this were the case, the reduced responsiveness caused by starvation could result in daytime plankton catches containing proportionately more starving larvae than those taken at night.

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Sea Turtle Strandings and Shrimp Fishing Effort in the Northwestern Gulf of Mexico, 1986-89

Charles W. Caillouet Jr.
Marcel J. Duronslet
Galveston Laboratory, Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA, Galveston, Texas 77551-5997

Andre M. Landry Jr.
Department of Marine Biology, Texas A&M University
Mitchell Campus, Pelican Island, Galveston, Texas 77553

Dickie B. Revera
Galveston Laboratory, Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA, Galveston, Texas 77551-5997

Donna J. Shaver
Padre Island National Seashore, National Park Service, U.S. Department of Interior
9405 South Padre Island Drive, Corpus Christi, Texas 78418

Kerry M. Stanley
Robert W. Heinly
Erich K. Stabenau
Galveston Laboratory, Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA, Galveston, Texas 77551-5997

Incidental capture of sea turtles in shrimp trawls is the most important human cause of sea turtle mortality (Magnuson et al. 1990). Offshore stocks of penaeid shrimp were discovered in the Gulf of Mexico in the mid-1930s, and expansion of the offshore shrimp fishery began in the late 1940s following World War II (Whitaker 1973, Krauthamer et al. 1984, Tetty and Griffin 1984, Rayburn 1989). The industry continued to expand and improve its fishing technology into the 1980s. During the same period when shrimping effort was increasing and harvesting technology was improving, the abundance of sea turtles declined (Magnuson et al. 1990).

Sea turtle strandings along coastal shorelines of the southeastern United States have been used as one index of mortality due to shrimping (Magnuson et al. 1990). An increase in sea turtle strandings during commercial penaeid shrimp fishing seasons and a decrease with the closing of these seasons have been observed on the Atlantic coast of the southeastern United States (Hillestad et al. 1978, Talbert et al. 1980, Ruckdeschel and Zug 1982, Booker and Ehrhart 1989, Schroeder and Maley 1989). The relationship between sea turtle strandings and shrimp fishing in the northwestern Gulf of Mexico has received less attention (Rabalais and Rabalais 1980, Amos 1989, Whistler 1989, Magnuson et al. 1990), although Texas and Louisiana together produce most (almost 74% during 1986–89) of the offshore (seaward of barrier islands) commercial catch of penaeid shrimp in the southeastern United States. In this study, we used product-moment correlation analysis to test the null hypothesis that there was no relationship between monthly sea turtle strandings and shrimp fishing effort in the northwestern Gulf of Mexico coast during 1986–89.

Sea turtles would not be captured in shrimp trawls if the temporal-spatial distributions of sea turtles and shrimp fishing effort did not overlap to some extent. However, we have no a priori reason to expect that temporal-spatial distributions of sea turtles and shrimp fishing effort match exactly. Shrimp trawling in the northwestern Gulf varies seasonally and spatially as related to the annual cycle of occurrence and abundance of short-lived penaeid shrimp (Kutkuhn 1962, Neal and Maris 1985). It is most intense during spring and summer when surface waters are warm. Shrimp spawn in the Gulf where the eggs hatch and larvae develop as they are carried toward the estuaries in spring and early summer. As postlarvae, shrimp enter the estuarine nursery areas where they grow for several months before emigrating to the Gulf and becoming vulnerable to the offshore shrimp fishery. There they continue to grow and migrate to deeper waters to spawn while being exploited by the fishery. In contrast, sea turtles are long-lived and can be exposed to mortality risks for decades. Based on strandings, commercial and recreational fishing bycatch, and aerial surveys, sea turtles are most abundant in the northwestern Gulf during spring or early summer, with a lesser peak in abundance in autumn (Hildebrand 1982, Fritts et al. 1983, Thompson 1988, Magnuson et al. 1990). Waters of the northwestern Gulf are foraging habitat for the turtles, and they are used as migratory routes when the turtles move northward in spring and southward in autumn (Hildebrand 1982, 1983). The most numerous species in the

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northwestern Gulf are the loggerhead *Caretta caretta* and Kemp's Ridley *Lepidochelys kempi* (Rabalais and Rabalais 1980, Thompson 1988, Amos 1989, Whistler 1989).

This study deals with monthly sea turtle strandings along shorelines and shrimp fishing effort seaward of shorelines in the northwestern Gulf. Strandings are observed for the most part on barrier beaches, so they can be summarized in linear distance units of shoreline. Shrimp fishing effort is reported as days fished within spatial units represented by shrimp statistical subareas and 5-fathom (fm, 9.1 m) depth intervals (Kutkuhn 1962, Patella 1975). To test the null hypothesis, we paired monthly strandings along segments of shoreline with monthly shrimping effort within 5-fm depth intervals in the adjacent offshore waters. This was done because it was expected that the farther offshore the shrimping took place, the less likely sea turtles impacted by such shrimping would reach the shoreline, due to combined effects of surface currents, winds, waves, tides, action by scavengers (e.g., sharks) and decomposition of turtle carcasses (Heinly et al. 1988, Murphy and Hopkins-Murphy 1989, Shoop and Ruckdeschel 1989, Whistler 1989). Also, it is possible that temporal-spatial distributions of sea turtles and shrimp fishing activities overlap only within certain depth intervals (Magnuson et al. 1990).

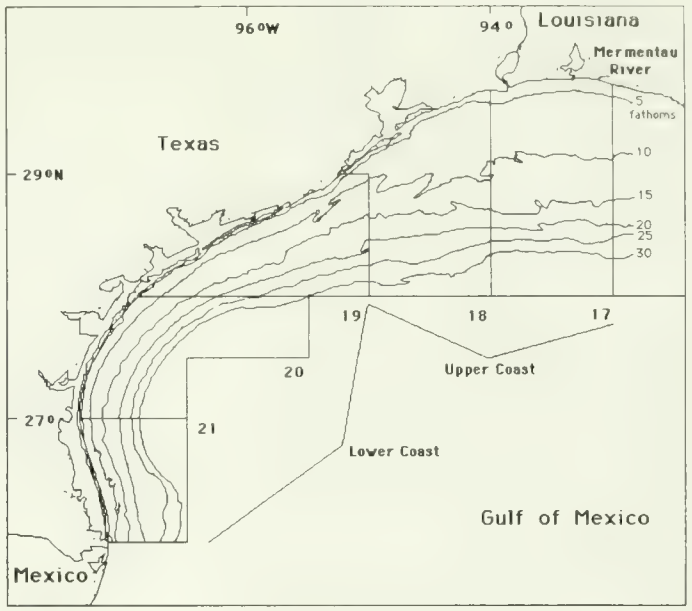

Figure 1

Boundaries of upper coast (shrimp statistical subareas 17–18) and lower coast (subareas 19–21) and 5 fm (9.1 m) depth intervals of the northwestern Gulf of Mexico (see Kutkuhn 1962, Patella 1975).

Materials and methods

Since 1980, sea turtle strandings along the coasts of the southeastern United States have been compiled by the Sea Turtle Stranding and Salvage Network (STSSN, Schroeder 1989). Shrimp fishing effort statistics in the Gulf have been compiled since 1956 (Kutkuhn 1962). Our analyses were based on data from 1986–89, including sea turtle strandings available from the STSSN database at the National Marine Fisheries Service's (NMFS) laboratory in Miami, Florida, and shrimp-fishing effort data available from the NMFS laboratory in Galveston, Texas.

Schroeder (1989) described the STSSN and procedures used to document sea turtle strandings. State coordinators review and verify the stranding data submitted by network participants, then forward them to the NMFS laboratory in Miami, Florida, where the database is maintained. The database is not independent of the distribution of human-induced mortality factors, temporal-spatial coverage is rarely uniform, and most beaches are surveyed by volunteers (Magnuson et al. 1990). To improve temporal-spatial coverage and supplement voluntary coverage, the NMFS Galveston Laboratory initiated year-round surveys along the coasts of southwestern Louisiana and Texas in 1986 (Heinly et al. 1988). Four-wheel-drive trucks, off-road motor cycles, or all-terrain vehicles were used to survey accessible gulfside shorelines at least once per month, from the Mermentau River, Louisiana, to the Texas–Mexico border (Fig. 1). The National Park Service surveyed the Padre Island National Seashore near Port Aransas, Texas, and the U.S. Fish and Wildlife Service and Texas Parks and Wildlife Department assisted in surveying Matagorda I. near Port O'Connor, Texas. Reconnaissance flights conducted at least once monthly were used to search for stranded turtles on San Jose I. near Corpus Christi, Texas.

For our analyses, sea turtle strandings (all species combined) in the northwestern Gulf of Mexico during 1986–89 were extracted from the STSSN database. Records of turtles caught by various commercial and recreational fishing methods were deleted. Also deleted were strandings of head-started (captive-reared) sea turtles, because their distribution is influenced to some extent by where they are released (Manzella et al. 1988, Fontaine et al. 1989).

The monthly sea turtle strandings and shrimp fishing effort were separated into two geographic zones: the upper coast (subareas 17–18) and lower coast (subareas 19–21). This was done because the upper coast has a wider continental shelf than the lower, so the distance a dead, sick, or injured sea turtle would have to travel from a particular depth interval to the shore is greater on the upper coast than on the lower (Fig. 1). Due to difficulty of access, the small portion of subarea 17 east of the Mermentau River in southwestern Louisiana was not surveyed for strandings, so approximately 86% of the coastline of the upper coast zone was surveyed for turtle strandings (Table 1). For this reason, we included in the upper coast zone only those turtle strandings that occurred west of the Mermentau River. We could not place a similar boundary restriction on the fishing effort data, so the eastern boundary of subarea 17 marked the eastern boundary of the upper coast in this regard. However, strandings and fishing effort were standardized to strandings per linear distance of shoreline and to days fished per unit area, respectively, so the exclusion of strandings east of the Mermentau River should have had little if any effect on our results.

Our analyses included fishing effort from the six 5-fm intervals between 0 and 30 fm (54.9 m) in shrimp statistical subareas 17–21. We did not include effort data beyond 30 fm, because only 6% of the shrimping effort on the upper coast and 8% on the lower coast occurred seaward of 30 fm during 1986–89 (Table 2).

Table 1

Extent of accessible shoreline surveyed for sea turtle strandings during 1986–89 compared with total shoreline within the upper and lower coasts of northwestern Gulf of Mexico[1].

Zone	Shrimp statistical subarea[2]	Shoreline		
		Accessible (km)	Total (km)	Percent of total
Upper coast	[3]17–18	212	245	86.5
Lower coast	19–21	408	420	97.1
Total	[3]17–21	620	665	93.2

[1] Derived from measurements made using dividers on National Ocean Service (NOAA) nautical charts.
[2] Figure 1; see also Kutkuhn (1962).
[3] Only the accessible shoreline west of the Mermentau River, Louisiana, was surveyed for strandings in subarea 17.

Table 2

Distribution of shrimp fishing effort on the upper and lower coasts of northwestern Gulf of Mexico by depth, 1986–89.[1]

Depth		Percent of shrimp fishing effort	
fm	m	Upper coast[2]	Lower coast[3]
0–5	0.0–9.1	28	5
5–10	9.1–18.3	27	13
10–15	18.3–27.4	16	20
15–20	27.4–36.6	10	26
20–25	36.6–45.7	7	18
25–30	45.7–54.9	6	10
30–50	54.9–91.4	6	8
Total		100	100

[1] Adapted from data provided by Frank Patella, NMFS Galveston Lab., pers. commun., June 1990.
[2] Shrimp statistical subareas 17 and 18 (Fig. 1; see also Kutkuhn 1962).
[3] Shrimp statistical subareas 19–21 (Fig. 1; see also Kutkuhn 1962).

Monthly sea turtle strandings within the upper and lower coasts were standardized by dividing them by distance of accessible shoreline (Table 1) in these two zones, respectively, to obtain the monthly turtle strandings per 100 km (S). We used the amount of surface area within shrimp statistical subareas and 5 fm depth intervals, as determined by Patella (1975), to standardize monthly fishing effort within the upper and lower coasts by depth interval. The surface area within a depth interval was usually greatest nearshore and decreased seaward in both zones (Fig. 1). For each 5-fm depth interval, monthly fishing effort in the upper and lower coast zones was divided by the surface area of the geographic unit (zone × depth interval) within which the effort occurred, to standardize effort to a measure of shrimping intensity. Standardized fishing effort per unit area (E) was expressed as days fished per 100 km^2.

Product-moment correlation analysis requires that the two variables have normal distributions. Neither standardized strandings (S) nor fishing effort (E) were normally distributed, as shown by large departures of their skewness and kurtosis coefficients from zero (Table 3). Therefore, we logarithmically transformed both variables, after adding 1 to each value of S and E (because some values were zero). The logarithmically transformed variables had skewness and kurtosis coefficients closer to zero, thus approaching normality. For each of the 12 combinations of two geographic zones and six depth intervals, product-moment correla-

Table 3

Descriptive statistics for untransformed and transformed monthly sea turtle strandings and shrimp fishing effort for the upper and lower coasts of northwestern Gulf of Mexico during 1986–89.

	Sea turtle strandings[1]		Shrimp fishing effort[2]	
	Upper coast	Lower coast	Upper coast	Lower coast
Untransformed				
n	48	48	288	288
Mean	4.16	3.18	13.26	17.82
Variance	43.15	9.15	509.35	374.03
Skewness coeff.	2.66	1.98	4.32	4.46
Kurtosis coeff.	7.60	4.50	22.37	31.84
Minimum	0.0	0.0	0.0	0.0
Maximum	31.7	14.7	170.1	197.4
Transformed[3]				
n	48	48	288	288
Mean	1.13	1.23	2.07	2.57
Variance	0.92	0.38	1.01	0.80
Skewness coeff.	0.66	0.36	0.51	−0.41
Kurtosis coeff.	−0.29	−0.05	0.23	0.44
Minimum	0.0	0.0	0.0	0.0
Maximum	3.49	2.75	5.14	5.29

[1]Per 100 km of accessible shoreline.
[2]Per 100 km^2 of surface area.
[3]To natural logarithms after addition of 1 to each observation.

tions between 48 pairs (12 months × 4 years) of ln (S + 1) and ln(E + 1) were determined.

Results

Scatter plots for geographic zones and depth intervals for which ln(S + 1) was significantly ($P<0.05$) correlated with ln(E + 1) are shown in Figure 2. On the upper coast, the three correlation coefficients, r, that differed significantly from zero were positive and occurred with fishing effort in the 0–5, 5–10, and 10–15 fm intervals. On the lower coast, r was significantly different from zero and positive only with fishing effort in the 5–10 and 10–15 fm intervals. These correlations indicated that turtle strandings increased as fishing effort increased in waters landward of 15 fm. Correlation coefficients for fishing effort in other depth intervals within the two zones did not differ significantly from zero.

The five significant correlations ($P<0.05$) were detected despite the relatively coarse temporal-spatial scale of the data sets (Fig. 2). Although they were of moderate strength, ranging from 0.327 to 0.512, even the lowest among them had a very small probability (P 0.0232) of occurring due to chance alone (Fig. 2). P was even smaller for the other four significant correlations. There was no significant ($P>0.05$) heterogeneity among the five correlation coefficients.

The means of the transformed strandings for the upper and lower coasts did not differ significantly (Table 3). However, the upper coast exhibited more months in which there were no strandings than did the lower coast (Fig. 2). The mean of transformed fishing effort on the lower coast was significantly higher than that for the upper coast, indicating a higher average fishing intensity on the lower than upper coast in waters landward of 30 fm.

Loggerheads and Kemp's Ridleys occurred most frequently in the strandings, followed by hawksbills *Eretmochelys imbricata*, greens *Chelonia mydas*, and leatherbacks *Dermochelys coriacea* (Table 4). Turtle strandings occurred year-round with peaks in April and May, and with a secondary peak in August. Annual strandings declined over the years covered by the study, with 417, 259, 188, and 183 strandings reported in 1986–89, respectively.

Discussion

The distributions of sea turtles and shrimp trawling must overlap to some degree because it is well documented that sea turtles are caught in shrimp trawls

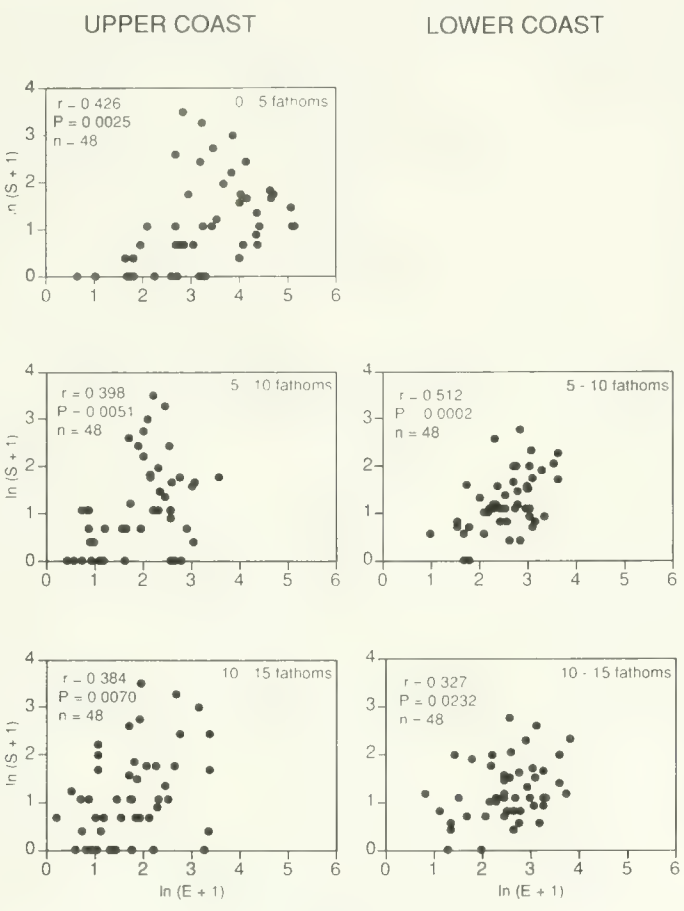

Figure 2

Scatter plots for significant ($P<0.05$) correlations between transformed monthly sea turtle strandings, ln(S + 1), and transformed monthly shrimp fishing effort, ln(E + 1), on upper coast (shrimp statistical subareas 17–18) and lower coast (subareas 19–21) of the northwestern Gulf of Mexico during 1986–89.

(Murphy and Hopkins-Murphy 1989, Magnuson et al. 1990). In fact, sea turtles may congregate in shrimping areas to feed on discarded bycatch (Shoop and Ruckdeschel 1982, Ruckdeschel and Shoop 1988). However, no cause-and-effect relationship between sea turtle strandings and shrimping has been demonstrated to date.

It is noteworthy that our analyses detected significant correlations despite the wide variation inherent in turtle stranding and fishing effort data. These significant positive correlations are circumstantial evidence of a linkage between strandings and shrimping, but do not demonstrate that the strandings were caused by shrimping. Strandings and shrimping occur year-round and both are strongly seasonal, with peaks during warm months. The correlations we detected are consistent with earlier findings that incidental capture in shrimp trawls is the major cause of sea turtle mortality associated with human activities, but it is also recognized that other fisheries, dredging, collisions with boats, oil-rig removal with underwater explosives, entrainment in power plants, and directed take contribute to sea turtle mortality at sea (Magnuson et al. 1990).

Interpretation of statistical relationships between sea turtle strandings and shrimp trawling activity is confounded by the dynamics of waterborne transport of stressed, injured, or dead turtles to stranding sites. Surface currents, winds, waves, tides, and scavengers, as well as conditions affecting the buoyancy of turtles, can affect their transport toward or away from shore (Murphy and

Table 4

Species composition of sea turtle strandings in the northwestern Gulf of Mexico by month, summed over years 1986–89.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Loggerhead *Caretta caretta*	9	10	46	146	95	33	40	37	31	29	19	20	515
Kemp's Ridley *Lepidochelys kempi*	0	6	36	82	48	36	27	51	23	22	17	9	357
Hawksbill *Eretmochelys imbricata*	0	1	2	0	1	5	4	15	18	14	2	5	67
Green *Chelonia mydas*	1	0	5	7	6	6	2	2	0	4	1	4	38
Leatherback *Dermochelys coriacea*	0	0	1	8	5	3	0	1	0	2	3	0	23
Undetermined	0	0	6	6	2	5	10	4	5	6	1	2	47
Total	10	17	96	249	157	88	83	115	77	78	43	40	1047

Hopkins-Murphy 1989, Shoop and Ruckdeschel 1989, Whistler 1989). In the northwestern Gulf, tidal currents move water toward shore, and waves and surface drift transport floating objects to the beach from longshore currents (Collard 1990, Collard and Ogren 1990). Swimming and diving abilities may be reduced in stressed or injured sea turtles, causing them to remain at or near the surface while being transported more or less passively. The longer a carcass remains in the water, the longer it would be subjected both to decomposition and scavengers which could cause it to disarticulate, release bloating gases, and sink. Not all turtles that become stranded are documented by the STSSN. Thus, reported strandings of sea turtles provide an incomplete measure of those that are killed or injured by humans or that succumb to natural mortality factors at sea (Murphy and Hopkins-Murphy 1989).

On the upper coast, significant correlations were observed in 0–15 fm where 71% of the shrimp fishing effort on the upper coast occurred during 1986–89 (Table 2, Fig. 2). Significant correlations were observed on the lower coast in 5–15 fm where 33% of the lower coast effort occurred. Such correlations suggest that the impact of shrimping on sea turtles may occur within 15 fm seaward of the coastline, and this is consistent with the conclusion by Magnuson et al. (1990) that incidental capture of sea turtles in shrimp trawls occurs for the most part in depths up to 27 m (15 fm). However, on the lower coast 5% of the shrimp fishing effort occurred in the 0–5 fm interval, and we observed no significant correlation for that interval.

It is neither practical nor cost-effective to attempt characterization of all conditions and factors that influence whether sea turtles become stranded and where and when they become stranded in relation to various causes of mortality, injury, stress, or illness at sea. However, year-round coverage is essential to monitoring temporal variations, and it provides biological samples, specimens for necropsy, and other information that can be compared with human activities and oceanographic variables in examining the causes of strandings.

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Trophic Relationship of Age-0 and Age-1 Walleye Pollock *Theragra chalcogramma* Collected Together in the Eastern Bering Sea*

Jill J. Grover

College of Oceanography, Oregon State University
Hatfield Marine Science Center, Newport, Oregon 97365

Walleye pollock *Theragra chalcogramma* a gadid endemic to the north Pacific, is one of the most important components of the Bering Sea food web (Smith 1981) and supports the largest single-species commercial fishery in the world (Megrey 1989). Although a number of studies have documented the food habits of larval (e.g., Kamba 1977, Cooney et al. 1980, Clarke 1978 and 1984, Kendall et al. 1987, Grover 1990), juvenile (e.g., Kamba 1977, Bailey and Dunn 1979, Cooney et al. 1980, Lee 1985, Grover 1990), and adult walleye pollock (e.g., Takahashi and Yamaguchi 1971, Bailey and Dunn 1979, Livingston et al. 1986, Dwyer et al. 1987, Bailey 1989), previous studies have generally pooled samples either over time or space. While pooled data adequately characterize large-scale patterns of prey utilization, small-scale patterns of between-year-class trophic relationships are best defined by fish that were collected together.

This study examined the trophic relationship of age-0 and age-1 pollock that were collected in a single haul in the southeastern Bering Sea. As pollock are known to be highly cannibalistic (Takahashi and Yamaguchi 1971, Bailey and Dunn 1979, Livingston et al. 1986, Dwyer et al. 1987, Bailey 1989), this study looked for evidence of cannibalism, as well as defined the size and taxa of prey that were ingested by the two year-classes.

Methods

Juvenile pollock were collected as one aspect of a survey of groundfish in the eastern Bering Sea in 1985 by the *Morning Star*, using a Marinovich midwater trawl (Walters et al. 1988). An examination of length-frequency distributions from these trawls, which principally targeted age-0 fish, revealed that age-0 (zeros) and age-1 fish (ones) were rarely collected together (Jim Traynor, NMFS Alaska Fish. Sci. Cent., Seattle, unpubl. data). Among stations where zeros and ones occurred in the same haul, comparable numbers of both year-classes were obtained at only one station. Coincidentally, although not all of the ones were saved, this was the only station where both ones and zeros were preserved. This collection was made from 0900 to 0920 hours on 3 August 1985, at station 95 (56° 11.17′N, 162°18.36′W), in the southeast shelf region. Gear depth averaged 20 m, and water temperature was 6.5°C. The fish were frozen at sea. In the laboratory, they were defrosted in 10% formalin to facilitate the simultaneous separation and fixation of the specimens. All the preserved specimens from this collection were analyzed.

This study examined the diet of 52 age-0 and 22 age-1 fish. Age groups were determined based on length, using the categories of Dwyer et al. (1987)—age 0, 1–130 mm; age 1, 131–220 mm, which were based on Smith's (1981) Bering Sea data. For each fish, total length was recorded and the stomach was removed. Stomach contents were dissected out and identified. Due to prey condition, only copepods could be consistently identified to species. Extremely well-digested copepods were identified largely by their size and shape. No distinction was made between copepodite and adult stages. Copepods eggs, *Calanus marshallae*, *Pseudocalanus* sp., *Centropages abdominalis*, *Metridia* sp., *Acartia* sp., and *Tortanus discaudatus* were identified. *Calanus marshallae* and *Metridia* sp. were >2 mm in length. All other copepod species were <2 mm. Other prey were identified as amphipods, euphausiid furcilia/juveniles, mysids, decapod larvae, and fish scales. Well-digested euphausiids were enumerated based on eye counts.

Food particle-size selection was examined by measuring widths of all prey items that were not severely digested or broken. Widths were recorded from a total of 7291 prey items.

Diet was analyzed in terms of numerical percent composition (%N), volumetric percent composition (%VOL), frequency of occurrence (%FO), and the index of relative importance (IRI = [%N + %VOL] × %FO) (Pinkas et al. 1971). Volumes were calculated from prey dimensions for zeros (Grover and Olla 1987), and were measured directly for ones.

Results

Little overlap was seen in the size of prey that were ingested by age-0 pollock, which ranged from 26 to 64 mm TL ($\bar{x}$ 49.4 mm, SD 9.6), and

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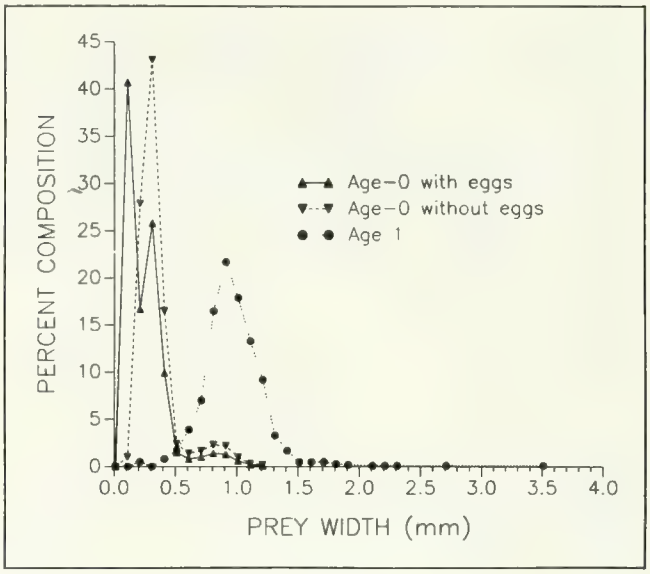
Figure 1

Size of prey ingested by age-0 and age-1 walleye pollock at station 95 (56°11.17′N, 162°18.36′W), in the southeastern shelf region of the Bering Sea, 3 August 1985. Age-0 data are plotted, including and excluding copepod eggs. Prey widths (in mm) were as follows: copepod eggs 0.11–0.20, *Calanus marshallae* 0.61–1.70, *Pseudocalanus* sp. 0.11–0.70, *Centropages abdominalis* 0.31–0.60, *Metridia* sp. 0.51–0.60, *Acartia* sp. 0.21–0.40, *Tortanus discaudatus* 0.31–0.50, amphipods 0.21–1.8, euphausiid furcilia/juveniles 0.21–3.50, mysids 0.41–0.50, decapod larvae 0.21–0.90. Fish scales were not included in this analysis, as their ingestion was deemed incidental.



by age-1 pollock, which ranged from 137 to 212 mm TL ($\bar{x}$ 162.8 mm, SD 16.32) (Fig. 1). Prey-size distributions were significantly different regardless of whether copepod eggs were included ($P<0.001$, Kolmogorov-Smirnov test; Conover 1980). Taxa of prey ingested by the two age-classes also differed (Table 1). Small copepods (0.21–0.50 mm width) and copepod eggs (0.11–0.20 mm width) comprised the bulk of the prey ingested by age-0 fish, while larger copepods and euphausiid furcilia (0.71–1.30 mm width) comprised the bulk of the prey ingested by age-1 fish.

Although euphausiid furcilia and juveniles made a substantial contribution to the diet of both age-classes, age-0 fish ingested smaller and/or earlier furcilia stages than did age-1 fish. Copepods comprised a major por-

Table 1

Composition of the diet of age-0 and age-1 walleye pollock *Theragra chalcogramma* in terms of index of relative importance (%IRI) and its components (%N, %VOL, and %FO). Values in parentheses exclude copepod eggs.

	Age-0				Age-1			
	%N	%VOL	%FO	%IRI	%N	%VOL	%FO	%IRI
Copepods								
Eggs	32.8	0.4	92.3	18.4				
Calanus marshallae	0.1 (0.2)	2.2 (2.2)	9.6	0.1 (0.1)	63.1	48.8	100.0	56.6
Pseudocalanus sp.	61.3 (91.3)	47.6 (47.8)	98.1	64.2 (81.8)	0.2	<0.1	13.6	<0.1
Centropages abdominalis	<0.1 (<0.1)	<0.1 (0.1)	3.8	<0.1 (<0.1)				
Metridia sp.	<0.1 (<0.1)	0.1 (0.1)	1.9	<0.1 (<0.1)				
Acartia sp.	0.1 (0.1)	<0.1 (<0.1)	5.8	<0.1 (<0.1)				
Tortanus discaudatus	<0.1 (<0.1)	<0.1 (0.01)	3.8	<0.1 (<0.1)				
Amphipods	<0.1 (<0.1)	<0.1 (<0.1)	3.8	<0.1 (<0.1	1.1	2.6	63.6	1.2
Euphausiid furcilia/juveniles	5.5 (8.2)	49.5 (49.7)	51.9	17.2 (18.0)	35.0	48.1	100.0	42.0
Mysids					<0.1	<0.1	4.5	<0.1
Decapod larvae					0.4	0.4	31.8	0.1
Fish scales					0.2	<0.1	27.3	<0.1

tion of the diet for both age groups, however age-0 fish primarily ingested small (<2mm in length) *Pseudocalanus* sp., while age-1 fish primarily ingested larger (>3mm) *Calanus marshallae* (Table 1).

Fish scales were observed in the stomachs of six age-1 fish. Only one scale was found in each stomach, and no other evidence of piscivory was observed. The scales were most likely ingested incidentally as a result of the collection process.

The mean number of prey ingested by age-0 fish was 134.8 (90.6 excluding copepod eggs), while age-1 fish ingested an average of 156.3 prey items. The incidence of feeding was 100% for both age groups.

Discussion

Based on two age and growth relationships (Nishimura and Yamada 1984, Yoklavich and Bailey 1989) and the timing of spawning in the southeast shelf region of the Bering Sea in 1985 (Mulligan et al. 1989), the age of age-0 pollock in this study was estimated to be 2–4 months. Assuming that the age-1 fish in this study were spawned as well as collected in the southeast shelf region, and then based on when spawning occurred in this region in 1984 (Hinckley 1987), the age of age-1 pollock was estimated to be 13–16 months.

At the time and place of this collection, diets of the two year-classes were divergent in terms of both prey size and taxa. Older, larger fish ingested larger prey. The importance of small copepods, notably *Pseudocalanus* sp., in the diet of age-0 pollock is consistent with previous studies (Kamba 1977, Cooney et al. 1980, Lee 1985, Grover 1990); however, one suborder of copepods, Cyclopoida, that was included in earlier dietary accounts was noticeably absent in the present study. Although, by most accounts, cyclopoids were not primary prey, Lee (1985) reported that for pollock between 20.0 and 24.9mm TL and 45.0 and 49.9mm TL, these copepods were either the foremost or second-most important prey in the southeastern Bering Sea. Differences between studies may reflect temporal or spatial patchiness of prey.

Large numbers of copepod eggs have previously been reported in the diet of juvenile pollock (Cooney et al. 1980, Lee 1985, Grover 1990). The eggs were probably ingested incidentally, as the dominant copepod in the diet of age-0 pollock, *Pseudocalanus* sp., carries its eggs (Corkett and McLaren 1978).

The diet of age-1 pollock was dominated by a large copepod, *C. marshallae*, and euphausiid furcilia and juveniles. While previous dietary accounts have also illustrated the importance of large copepods, other specifics of diet apparently vary seasonally and spatially. Bailey and Dunn (1979) found that in the eastern Bering Sea, amphipods replaced euphausiids in the diet of pollock <24cm in the summer of 1974. Dwyer et al. (1987) reported that copepods were the only prey ingested by pollock <30cm in the southeastern Bering Sea during the summer, although in the northwestern Bering Sea euphausiids and larvaceans were also a part of the summer diet. The absence of copepod eggs from the diet of age-1 fish is consistent with the fact that *C. marshallae* females broadcast rather than carry eggs (Peterson 1980).

Another trophic relationship reported for these two year-classes is cannibalism (Livingston et al. 1986, Dwyer et al. 1987). While adult pollock cannibalize age-0 pollock to some extent during all seasons in the eastern and southeastern Bering Sea, age-1 pollock (<30cm) have been observed to be cannibalistic only during autumn (Livingston et al. 1986, Dwyer et al. 1987). In the present study, based on a collection in summer, no conclusive evidence of piscivory or cannibalism was observed. Cannibalism has been shown to be highest when the vertical distribution patterns of juveniles and adults overlap (Bailey 1989). As this collection was not vertically discrete, the extent to which vertical distributions of age-0 and age-1 pollock overlapped at station 95 is unclear. However, based on the short duration and nature of this collection, i.e., that it targeted a hydroacoustic trace at a specific depth (Jim Traynor, NMFS Alaska Fish. Sci. Cent., Seattle, pers. commun. May 1991), then, minimally, vertical juxtaposition of the two year-classes is suggested. In which case, the present data indicate that when appropriate alternate prey are available, the juxtaposition of two juvenile year-classes can occur without cannibalism resulting. At station 95 in the eastern Bering Sea in August 1985, age-0 and age-1 pollock had a trophically neutral relationship: the food habits of each year-class did not impinge upon nor imperil the other.

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Diet Composition of Pilot Whales *Globicephala* sp. and Common Dolphins *Delphinus delphis* in the Mid-Atlantic Bight during Spring 1989

William J. Overholtz
Gordon T. Waring

Woods Hole Laboratory, Northeast Fisheries Science Center
National Marine Fisheries Service, NOAA, Woods Hole, Massachusetts 02543

Several species of marine mammals are found in large numbers along the eastern United States and are seasonally abundant in the Mid-Atlantic Bight (Kenny et al. 1983, Payne et al. 1984). Concentrations of pelagic fishes also occur in the Mid-Atlantic Bight area during winter and spring and are preyed upon by marine mammals, seabirds, and piscivorous fishes (Overholtz et al. 1991). Pilot whales *Globicephala* sp. and common dolphins *Delphinus delphis* are two of the more abundant marine mammals found in the area and potentially account for 30% of the total consumption of pelagic fishes by all cetaceans in the region (Overholtz et al. 1991). Detailed analyses of diet composition, specific rations, and size and age composition of prey consumed by marine mammals are sparse, since few healthy, recently dead animals are available for analysis. Most information on the diet composition of marine mammals found in the northwest Atlantic is from strandings, data from commercial whaling operations in Canada in the 1950s (Sergeant 1962), or incidental kills in commercial fishing operations.

Pilot whales were thought to feed extensively on short-finned squid *Illex illecebrosus* and secondarily on Atlantic cod *Gadus morhua* (Sergeant 1962, Mercer 1975), but more recently have been shown to feed on several other pelagic fishes and squids in the northwest Atlantic. In the area off New England and the Mid-Atlantic, pilot whales coincide with short and long-finned squid as well as Atlantic mackerel and butterfish *Peprilus triacanthus* (Smith et al. 1990). Pilot whales and common dolphins captured in foreign fishing operations during the 1980s were feeding on Atlantic mackerel and long-finned squid during winter and spring in the Mid-Atlantic region (Waring et al. 1990).

Studies quantifying fish consumption in the pelagic ecosystem off the eastern United States have suggested that marine mammals may be important predators (Kenny et al. 1983, Overholtz et al. 1991). Large numbers of marine mammals may reside in this region, but the impact of these predators on prey resources is difficult to assess since so few studies have documented the seasonal prey, ration size, and other dynamics of mammalian diets.

The objectives of this study were to describe prey types and quantities found in pilot whales and common dolphins, investigate the age distribution of their fish prey, and to assess the trophic role of these two mammals in the region. These data are necessary for understanding the sources and magnitudes of predation on fish resources at the age-specific level, a critical component of ecosystem modeling.

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Fishery Bulletin, U.S. 89:723–728 (1991).

Methods

Stomachs were collected from 5 pilot whales and 4 common dolphins that were taken incidental to fishing operations conducted in the Mid-Atlantic region of the eastern United States. Data were collected by U.S. observers on foreign vessels in the offshore Atlantic mackerel trawl fishery. Animals were obtained on five separate occasions from 19 March 1989 to 17 April 1989 in the Hudson Canyon area (Fig. 1). Sampling involved morphometric measurements of total length, girth, various fin and flipper measurements, determination of sex of the mammals, and excision of the stomach which was frozen for later analysis.

Contents of the thawed stomachs were sorted to the lowest taxonomic group possible and wet weights were obtained to the nearest gram. Individual fish were weighed separately, while squid were weighed as a group. Mantle length of squid was measured to the nearest mm (Lange and Johnson 1981). Fork length was recorded for mackerel to the nearest mm. Skull shape and otoliths were used to identify the Atlantic mackerel which were in various stages of digestion. Long-finned squid were identified by examining mantles, pens, and beaks. Mackerel were aged by mounting whole otoliths in resin and counting growth layers at 60× magnification (Dery 1988).

In some cases mackerel were fragmented usually at the caudal peduncle. Length of these specimens was estimated by realigning fragments or by visual reconstruction of the missing pieces through observations of fresher specimens along with a general knowledge of relative body proportions in the caudal region. Measurement error based on this method is unlikely to be greater than 10–20 mm (3–6% of total body length), and is accurate enough for estimating the relative

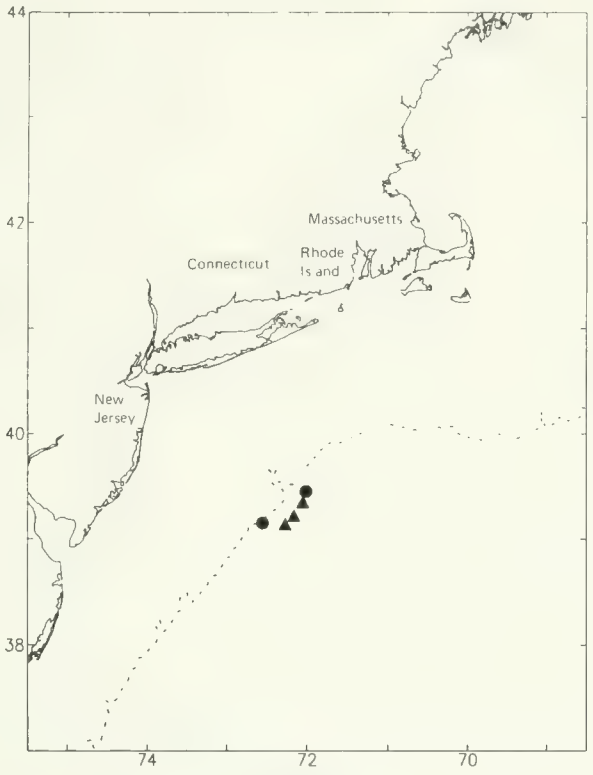

Figure 1

Mid-Atlantic region of the northeastern United States with locations in the Hudson Canyon area (north lat., west long.) of incidental captures of pilot whales (triangles) and common dolphins (circles) along the 100-m contour (dotted line) during March–April 1989.

size distribution of the prey. Partially digested mackerel were also weighed individually when possible, resulting in a minimum estimate of individual weight.

The food habits data were summarized to show diet characteristics of each animal. The age composition data for mackerel from stomach contents were summarized by percent number-at-age and compared with year-class size information from virtual population analysis (VPA) (unpubl. data) to discern if diet composition of the mammals was similar to age composition in the stock. To facilitate this comparison, a food selection index was calculated as

$$Li = ri - pi \quad (1)$$

where ri is the proportion of prey i in the stomach, and pi is the proportion of prey i in the environment (Strauss 1979). This index ranges from -1 to $+1$ with 0 indicating no predator preference (Strauss 1979).

In addition, the theoretical daily energy budget of each individual animal was compared with the estimated caloric value of the food in the stomach. Individual weights of pilot whales and common dolphins were obtained from length-weight equations (Lockyer 1991, J. Mead, Smithson. Inst., Wash. DC, pers. commun. 1989). Individual daily caloric requirements (Kcal/day) were estimated from a relationship between resting metabolism and body weight (Lockyer 1981), with a correction for assimilation and activity (Hinga 1979, Kenny et. al. 1983). The energy values of each animal's stomach contents were estimated by converting prey weight to caloric content (Kcal) by using conversion rates of 1.43 Kcal/g for Atlantic mackerel and 1.34 Kcal/g for long-finned squid (Steimle and Terranova 1985).

Results

Pilot whale and common dolphin fed on Atlantic mackerel and long-finned squid during March and April of 1989 (Table 1). A few otoliths of hake *Merluccius* sp. were found in two pilot whales and one common dolphin. The condition of prey items in both species ranged from slight to well digested, but could be identified to species. In contrast to previous years (Waring et al. 1990), none of the stomachs contained fresh material, although all the mackerel in pilot whale no. 1 were only slightly digested (Table 1). This suggests that all the animals had fed prior to being captured in the trawl.

The pilot whales that were examined were between 400 and 471 cm, both male and female (Table 1). Total weight of stomach contents in pilot whales were in the range 620–7200 g and averaged 2555 g (Table 1). Atlantic mackerel averaged 71% of the wet weight of stomach contents, and long-finned squid comprised the remaining (Table 1). Atlantic mackerel dominated the diets of individual pilot whales in terms of percent weight, except pilot whale no. 2 which fed exclusively on long-finned squid (Table 1). The estimated mean length of mackerel were in the range 355–460 mm, with mean weights of 332–426 g, and modal age of 7 years. (Table 1). Mean lengths of long-finned squid were 88–146 mm and weights 32–93 g, although both of these measurements are probably underestimates since all squid were at least partially digested.

The four common dolphins were also medium-sized individuals of 170–213 cm (Waring et al. 1990) of both sexes (Table 1). They fed primarily on mackerel, although the remains of long-finned squid were present in the stomachs of two individuals (Table 1). It was impossible to measure any mackerel found in the stomachs since they were well digested, and they were

Table 1

Summary of stomach contents of 5 pilot whales and 4 common dolphins collected in March–April 1989 off the northeastern United States. AM = Atlantic mackerel, LS = long-finned squid.

Predator				Prey										
				Species (*N*)		Modal age	Mean length (mm)[1]		Mean wet weight (g)		Total weight (g)[2]		% weight	
Species	Specimen no.	Length (cm)	Sex	AM	LS	AM	AM	LS	AM	LS	AM	LS	AM	LS
Pilot whales														
	1	401.0	M	16	4	7	354.8	88.3	426.8	93.3	6829.4	573.0	94.8	5.2
	2	400.0	F	—	43	—	—	145.8	—	52.8	—	2268.7	—	100.0
	3	463.0	F	1	8	—	460.0	102.0	359.4	32.8	359.4	262.6	57.8	42.2
	4	440.0	M	2	—	—	360.0	—	332.3	—	664.5	182.0	78.5	21.5
	5	471.0	F	3	13	7	378.3	128.8	424.6	43.3	1273.7	563.1	69.3	30.7
Total				22	68	7	363.2	134.0	414.9	51.0	9127.0	3649.4	71.4	28.6
Common dolphins[3]														
	1	170.0	M[4]	4	—	7	—	—	186.9	—	747.5	—	100.0	—
	2	207.0	F	6	—	7	—	—	403.3	—	2420.0	—	100.0	—
	3	200.0	M	4	—	5	—	—	294.3	—	1177.0	—	100.0	—
	4	213.0	M	3	—	7	—	—	113.0	—	339.0	—	100.0	—
Total				17	—	—	—	—	—	—	4683.5	—	100.0	—

[1] Only lengths of measurable prey are included here.
[2] Includes weight of all stomach contents for this species.
[3] Specimens 3 and 4 had long-finned squid pens in the stomach from a previous meal.
[4] Atlantic mackerel found in the stomachs could not be measured or weighed individually due to the state of digestion.

identified by otoliths. The estimated mean weight of mackerel was 113–403g, and modal age was 7 years (Table 1).

The age distribution of mackerel was similar in pilot whales and common dolphins, with age groups 4–8 representing the bulk of the prey items. Age 7 was the dominant age group in the diet of both predators comprising 71% and 56% of the mackerel eaten by pilot whales and common dolphins, respectively (Table 2). This age group is from the very large 1982 year-class of mackerel (Table 2). Values from the food selection index comparing percent in stomachs with the stock, indicate that both predators may have concentrated on mackerel from age group 7. Positive index values were also obtained for ages 5–8 for common dolphins (Table 2).

A comparison of theoretical daily energy budgets of individual animals with the caloric content observed in stomach contents revealed that, in most cases, the diets represented only a small fraction of the daily requirement (Table 3). The amount of observed prey in pilot whale stomachs would supply 1.8–28% of the daily theoretical requirement, and 6–44% in common dolphins.

Discussion

Pilot whales and common dolphins captured during fishing operations for mackerel in 1989 appeared to feed primarily on mackerel and long-finned squid, although three specimens contained otoliths of hake *Merluccius* sp. Waring et al. (1990) reported on the diet of 33 common dolphins collected from 1986 to 1988 during the same time period and found similar prey items, including the presence of a few hake otoliths. Hake may either be consumed infrequently or the otoliths are entering the stomachs through other prey such as long-finned squid.

Capture location of the two mammal species was localized (Fig. 1), but captures extended over a 30-day period. The data may represent a normal pattern for winter-spring feeding or an attraction to fishing activity. This study suggests that the captured mammals were not entirely dependent on fishing operations for prey, since long-finned squid were present in stomachs but not in catches by commercial vessels.

Results from the food selection index analysis suggest a slight positive selection for ages 5,6, and 8 by common dolphins, and moderate selection for age 7 by both cetaceans (Table 2). Statistical tests are possible with this index (Ready et al. 1985); however, they

Table 2

Comparison of abundance of Atlantic mackerel in the sea with numbers in stomach samples from 5 pilot whales and 4 common dolphins taken incidentally during March–April 1989 off the northeastern United States.

		Mackerel		Pilot whales			Common dolphins		
Age	Year-class	Abundance[1]	% of population	*N*	% in stomachs	Li[2]	*N*	% in stomachs	Li[2]
2	87	584	14.4	0	0.0	−0.144	0	0.0	−0.144
3	86	471	11.6	1	4.8	−0.068	0	0.0	−0.116
4	85	823	20.3	2	9.5	−0.108	1	6.3	−0.140
5	84	199	4.9	0	0.0	−0.049	2	12.5	0.076
6	83	107	2.6	1	4.8	0.022	2	12.5	0.099
7	82	1538	38.0	15	71.4	0.334	9	56.3	0.183
8	81	245	6.1	1	4.8	−0.013	2	12.5	0.064
9	80	38	0.9	0	0.0	−0.009	0	0.0	−0.009
10	79	5	0.1	0	0.0	−0.001	0	0.0	−0.001
11	78	30	0.7	0	0.0	−0.007	0	0.0	−0.007
12	77	4	0.1	0	0.0	−0.001	0	0.0	−0.001
13	76	7	0.2	1	4.8	0.046	0	0.0	−0.002
Total		4051	100.0	21[3]	100.0		16[3]	100.0	

[1] Millions of fish (unpubl. data).
[2] Linear index of food selection (Strauss 1979).
[3] Numbers reported here are 1 less than in Table 1, because 1 fish from each cetacean could not be aged.

Table 3

Comparison of daily estimated ration with amount of food in stomachs for 5 pilot whales and 4 common dolphins taken incidentally during March–April 1989, off the northeastern United States. AM = Atlantic mackerel, LS = long-finned squid.

		Predator			Prey					
					Total weight (g)		Caloric content[3] (Kcal)			
Species	Specimen no.	Length (cm)	Weight[1] (kg)	Ration[2] (Kcal/day)	AM	LS	AM	LS	Total caloric content (Kcal)	% of ration
Pilot whale										
	1	401.0	760	37184	6829.4	373.0	9766	500	10266	27.6
	2	400.0	725	35844	–	2268.7	–	3040	3040	8.5
	3	463.0	1049	47841	359.4	262.6	514	352	866	1.8
	4	440.0	957	44541	664.5	182.0	950	244	1194	2.7
	5	471.0	1095	49487	1273.7	563.1	1821	755	2576	5.2
Common dolphin										
	1	170.0	62	5236	747.5	–	1069	–	1069	20.4
	2	207.0	104	7850	2420.0	–	3461	–	3461	44.1
	3	200.0	94	7253	1177.0	–	1683	–	1683	23.2
	4	213.0	110	8203	339.0	–	485	–	485	5.9

[1] Obtained from a length-weight relationship from Lockyer (1991) for pilot whales, and from J. Mead (Smithson. Inst., pers. commun. 1989) for common dolphins.
[2] From a relationship between resting metabolism and body weight (Lockyer 1981) and a correction for assimilation and activity (Kenny et al. 1983).
[3] Obtained by converting prey weight to Kcal by using 1.43 Kcal/g for Atlantic mackerel and 1.34 Kcal/g for long-finned squid (Steimle and Terranova 1985).

cannot be used on these data since current methodology is not available to calculate the variance of stock size estimates based on the VPA. Mackerel school by size-age groups, and the older fish tend to be distributed farther offshore than younger fish (Sette 1950). The observed feeding pattern may reflect the absence of smaller, younger fish offshore and low abundance of older, larger fish (Table 2).

The age distribution of mackerel in the diet indicates that these smaller odontocetes are probably feeding on the older age groups of mackerel during the winter–spring season (Table 2). This is in contrast to fish predators such as Atlantic cod and spiny dogfish *Squalus acanthias* that feed on younger age groups of mackerel (Overholtz et. al. 1991). Smaller mouth size of the predatory fish probably limits their prey size. Marine mammals can feed on larger prey and are in direct competition with fisheries targeting these older, larger fishes (Overholtz et. al. 1991).

Energy budget calculations, when compared with caloric values of stomach contents, indicate that both pilot whales and common dolphins may need to feed several times per day to obtain their needed ration (Table 3). Although the analysis may be biased low and therefore somewhat conservative, it does suggest that the observed stomach contents may represent only a percentage of estimated daily requirement (Table 3). Therefore, stomach data from these cetaceans may underestimate the actual impact on prey resources.

The role of marine mammals has not been adequately described in many ecosystems since many populations are remote and the autopsy of fresh animals is infrequent. In the northwest Atlantic, most information on the diet composition of cetaceans has come from stranded incidentally captured animals, and commercial harvests (Sergeant 1962, Mercer 1975, Sergeant et al. 1980) or observations of codistributed mammals and prey (Overholtz and Nicolas 1979, Payne et al. 1986, Mayo et al. 1988, Smith et al. 1990). In the future, collection of more data on feeding behavior, prey species consumed, and overlapping distributions of mammals and prey on a seasonal basis, as well as a thorough sampling of incidental captures, will be necessary if the trophic role of marine mammals is to be determined. An intensive survey of the entire mammal population during this winter-spring period and in other seasons, along with some observations of activity around fishing vessels, would help determine how important the mackerel fishery is in influencing the behavior of smaller cetaceans.

Acknowledgments

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Relation between Hook Depth and Fishing Efficiency in Surface Longline Gear

Juan Carlos Rey

Spanish Institute of Oceanography, Coastal Center of Fuengirola
P.O. Box 285, Fuengirola, Málaga, Spain

Ramon Muñoz-Chápuli

Department of Animal Biology, Faculty of Science
University of Málaga, 29071 Málaga, Spain

Surface longline gear can operate at a range of depths, and hooks placed at different depths can have different fishing efficiencies, depending on the target species and its behavior. With better knowledge of the relationship between hook depth and hook catch rates, catch rates could be improved by placing the majority of hooks at the depth range preferred by the target species. However, little data exist on this subject in the literature, probably due to the difficulty of obtaining information about the differential catch rates of each hook and in estimating absolute depths. Yoshihara (1951) reports that the vertical distributions of *Thunnus orientalis* and *Germo germo* caught by longline are bell-shaped, suggesting different water temperature preferences by each species. Suzuki et al. (1977) state that the same fishing methods and longline gear are frequently used regardless of the areas and species. These authors also remark that there have been no systematic studies on the vertical distribution of tunas and billfishes. A well-known exception was in the 1970s when the Korean and Japanese commercial longliners changed from regularly using the gear near surface to fish for bigeye tuna to using it at greater depths to target yellowfin tuna *Thunnus albacares* (Saito 1975, Suzuki et al. 1977, Yang and Gong 1987). There is also some information about the behavior and depth range of swordfish *Xiphias gladius* (Carey and Robison 1981) and blue shark *Prionace glauca* (Sciarrota and Nelson 1977) in the literature.

Our aim was to obtain a simple, statistical relationship between the fishing efficiency of each hook in a basket (a stretch of longline between two floats) and its relative depth. We used data from a tropical eastern Atlantic Ocean fishing trip, where commercial longline gear was regularly used by southern Spanish fishermen to catch swordfish as a primary target species and mako shark *Isurus oxyrinchus* as the most valuable bycatch species. The study was carried out on the gross catch, in which the target species, swordfish and mako shark, comprised only 5–21% of the total catch.

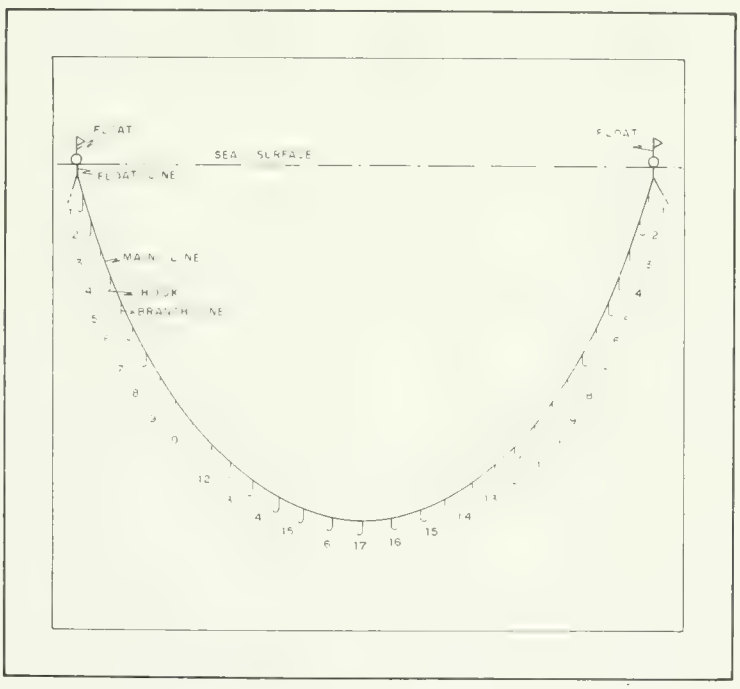

Figure 1
Scheme of the longline used in this study. Numbers show hook position.

Methods

The longline gear employed in this study consisted of "baskets" between floats (Fig. 1). Float lines measured about 7 m, while the main line within each basket measured about 1200 m. Branch lines (33 per basket) were 15 m long. This standard gear design is modified by

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Spanish fishermen operating in the Atlantic Ocean and Mediterranean Sea according to their experience and customs.

A total of 706 baskets were deployed during 16 nocturnal fishing operations in April 1985, located between 10°27′–11°42′N lat. and 17°17′–17°45′W long. Each fish was identified, sexed, and measured. The hook number within each basket was also recorded. A summary of the species caught and their abundances will be reported in a separate paper (Rey and Muñoz-Chápuli, in press).

Maximum depth reached by the deepest hook (position 17) was estimated to be between 370 and 460 m, using the theoretical procedure described by Yoshihara (1951, 1954).

Hook catch rates (HR) per 100 hooks were calculated using:

HR = (number of fish caught/number of hooks set in the jth position) × 100.

A total of 1412 hooks were set in positions 1–16, while 706 hooks were set in position 17.

Results and discussion

Table 1 shows the hook catch rates (HR) obtained for total catch, swordfish, and mako shark which was the most valuable species in the bycatch. Composition of bycatch is also presented in this table. A maximum HR of more than 5 fish/100 hooks for the total catch was observed between hook positions 3 and 5 (Fig. 2A). Values were generally lower beyond position 10, where the HR values were 2.8–4.6 fish/100 hooks.

The highest HR for swordfish was recorded at hook positions 3–13 (Fig. 2B). Mako sharks were captured mainly between hook positions 5 and 8 (Fig. 2C). They were never captured at hook position 15 or 17.

Table 1 includes the proportion of bycatch (total catch less swordfish and mako shark). As can be observed in Figure 2D, hook positions 14–17 show the highest HRs for the bycatch proportion. This indicates that these lower hooks are less effective for catching both swordfish and mako shark, which are caught in higher numbers on hooks 3–13.

Few data exist in the literature to compare with our results. Suzuki et al. (1977) compared catches of regular (to 150 m depth) and deep (250–300 m depth) tuna longlines in the western and central equatorial Pacific Ocean. They recorded a higher HR for swordfish using shallower gear. Carey and Robison (1981) observed, through radio-tracking, that in the Atlantic Ocean swordfish follow isoluminic trajectories. They were located in depths of 400–600 m during the day and 0–170 m at night. However, in the Pacific Ocean the depth range recorded for swordfish was 50–100 m during the day and 0–70 m at night. This could explain the slightly deeper maximum depth of fishing efficiency we recorded in the tropical eastern Atlantic Ocean, compared with that of Suzuki et al. However, Yang and Gong (1987) found a higher swordfish catch per unit of effort around 150 m in the central Atlantic (0°–10°N).

Table 1

Hook catch rates of total fish, swordfish *Xiphias gladius*, and mako shark *Isurus oxyrinchus* during 16 nocturnal fishing operations in the tropical eastern Atlantic Ocean. Right column shows proportion of "other species" in the total catch. Correlation coefficients (r) from the linear relationship between hook position and HR/proportion other species are also shown. HR = no. hooks with catch/no. hooks set in jth position × 100 (see text).

Hook position	Hook catch rates (fish taken/100 hooks)				Proportion of other species (%)
	Total fish	Swordfish	Mako shark	Other species*	
1	4.46	0.35	0.28	3.83	86
2	4.18	0.35	0.21	3.62	87
3	5.67	0.92	0.21	4.54	80
4	5.10	0.57	0.21	4.32	85
5	5.24	0.64	0.35	4.25	81
6	4.39	0.42	0.07	3.90	89
7	4.96	0.71	0.28	3.97	80
8	3.68	0.42	0.35	2.91	79
9	4.81	0.57	0.14	4.10	85
10	4.81	0.57	0.21	4.03	84
11	3.47	0.50	0.21	2.76	80
12	4.53	0.64	0.21	3.68	81
13	4.18	0.64	0.07	3.47	83
14	3.68	0.07	0.21	3.40	92
15	4.60	0.50	0.00	4.10	89
16	3.89	0.42	0.07	3.40	87
17	2.83	0.14	0.00	2.69	95
r	−0.59**	−0.35	−0.63**		0.43

* 55.9% *Carcharhinus signatus*, 17.0% *C. falciformis*, 9.3% *Alopias superciliosus*, 7.8% *Prionace glauca*, 5.5% *Mobula* sp., 1% *Sphyrna lewini*. Less than 1%: *Sphyrna couardi, S. mokarran, S. zygaena, Centrophorus granulosus, Galeocerdo cuvieri, Isurus paucus, Carcharhinus plumbeus, Thunnus obesus, Lepidocybium solanderi, Alepisaurus ferox.*

** $P<0.01$.

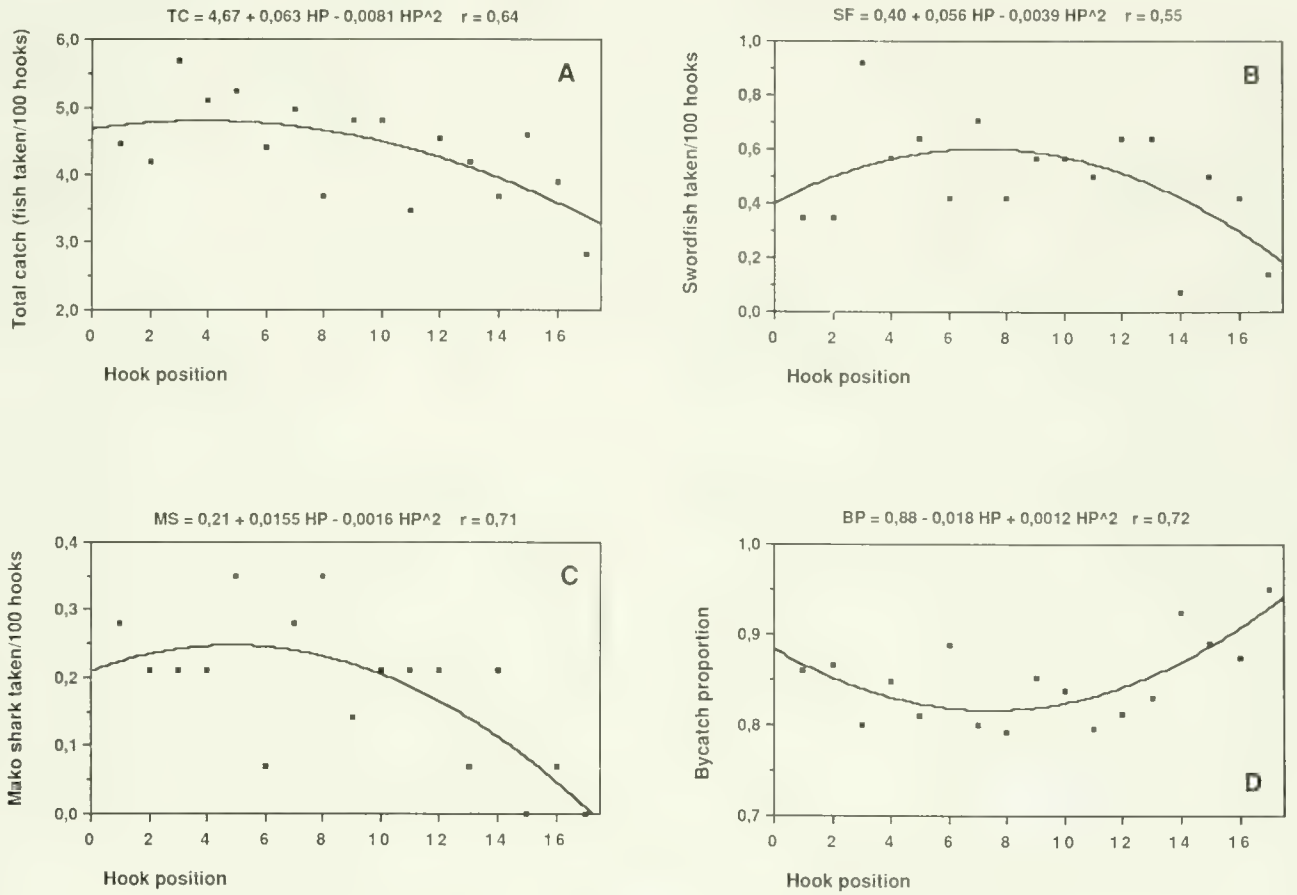

Figure 2

Relationships of hook catch rates to hook position for the total catch (A), swordfish (B), and mako shark (C). (D) Relationship between bycatch proportion (total catch less swordfish and mako shark) and hook position.

The ratios described in the results suggest that a better catch could be obtained with a different basket shape. Thus, by eliminating the deepest hooks, a smaller basket would be produced with most of the hooks placed in the depth range that demonstrated better fishing efficiency.

It should be noted that these data are valid only for particular spatial-temporal conditions, and they depend on environmental and biological variables such as temperature, light level, current, behavior, and food availability. Notwithstanding, our results show that further comparative and experimental studies on longline gear design could significantly improve the yield of fishing operations.

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Growth and Mortality of King Mackerel *Scomberomorus cavalla* Tagged in the Southeastern United States

Frederick C. Sutter III

Florida Marine Research Institute, Department of Natural Resources
100 Eighth Avenue SE, St. Petersburg, Florida 33701-5095

Roy O. Williams

Florida Marine Fisheries Commission, 2540 Executive Circle West
Suite 106, Tallahassee, Florida 32301

Mark F. Godcharles

Southeast Region, National Marine Fisheries Service, NOAA
Duval Building, 9450 Koger Boulevard, St. Petersburg, Florida 33702

King mackerel *Scomberomorus cavalla* is a heavily exploited coastal pelagic scombrid that has received considerable attention from research and management concerns throughout the southeastern United States (Gulf of Mexico and South Atl. Fish. Manage. Counc. 1985). Age-length data from analyses of otoliths have recently been used to estimate growth and mortality of the Gulf of Mexico migratory ("stock") group (Manooch et al. 1987) and growth of the Atlantic group (Collins et al. 1988). Previous studies did not differentiate between Gulf and Atlantic groups (Beaumariage 1973, Johnson et al. 1983). Length-increment (tag return) data can also be used to estimate growth and mortality; however, the growth parameter values generated from these data may not be directly comparable with those developed using age-length information (Francis 1988). In this report, we present estimates of growth and mortality based on mark-recapture data for both the Gulf and Atlantic king mackerel groups.

Table 1

Number of king mackerel *Scomberomorus cavalla* tag releases off southeastern United States by year, 1975–79, and migratory group.

	Location and month of release/Migratory group			
Year	Ft. Pierce, FL December–March/ Gulf of Mexico[1]	Florida Keys February, March/ Gulf of Mexico[2]	Jupiter, FL May, June/ Atlantic[3]	S. Carolina May, June/ Atlantic[4]
1975	880	–	372	–
1976	1904	974	1318	–
1977	1666	844	588	–
1978	1966	776	396	–
1979	–	–	–	809
Total	6416	2594	2674	809

[1] For all years except 1975, the annual totals for the Ft. Pierce area include December releases of the previous year. Northern boundary of the release area was defined by 28°45′N lat. and the southern boundary by 27°07′N lat.
[2] Eastern boundary of the release area was defined by 81°10′W long., southern boundary by 24°10′N lat., western boundary by 83°30′W long., and northern boundary (Gulf of Mexico only) by 27°00′N lat.
[3] Northern boundary of the release area was defined by 27°07′N lat. and southern boundary by 26°19′N lat.
[4] Northern boundary of the release area was defined by 33°50.0N lat. and southern boundary by 32°03.0′N lat.

Methods

King mackerel captured by hook-and-line were marked with internal anchor tags along the southeastern United States from South Carolina to the Florida Keys during 1975 to 1979 (Sutter et al. 1991). Tagged fish were assigned to the Gulf or Atlantic migratory groups (Table 1) based on location and date of release using current stock definitions (Powers and Eldridge 1983). King mackerel tag returns that did not show negative growth (based on reported length) were grouped into 30-day intervals based on time-at-large. The mean change in length between release and recapture and the mean time-at-large were determined for each 30-day period. Use of means within blocks eliminated the unequal weighting caused by the large number of fish returned less than one year after release, or by any periodicity in seasonal recaptures. These values were used to estimate the von Bertalanffy growth parameters L_∞ (asymptotic size) and K (growth rate constant) using a non-linear solution (SAS 1985) of Fabens (1965) method. We did not have enough fish to partition our data further to describe growth parameters for male and female king mackerel.

Mortality estimates were made separately for Gulf of Mexico and Atlantic king mackerel groups.

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Table 2

Tag-recapture matrix for Gulf of Mexico and Atlantic migratory groups of king mackerel *Scomberomorus cavalla*. Year reported represents a 12-month time interval from time of release.

Year released	No. released	Year reported 76/77	77/78	78/79	79/80	80/81	81/82	82/83	83/84
Gulf of Mexico group									
1976	2878	120	58	26	7	4	3	–	–
1977	2510		108	62	22	12	3	–	–
1978	2742			104	66	25	12	8	2
Atlantic group									
1976	1318	34	15	7	6	2	–	–	–
1977	588		25	16	12	8	3	–	–
1979	809				12	14	7	6	1

Regression analysis techniques (Gulland 1969) were used to estimate the average annual survival rate for each tagging year by grouping returns into 12-month intervals beginning with month of release (December–March for the Gulf of Mexico group, and May–June for the Atlantic group) (Table 2). Fish recaptured within 30 days of release were not included in our analysis, which allowed tagged fish to recover from tagging and reduced the effect of short-term tagging mortality on our estimates of survival rate. Only the Gulf stock had sufficient numbers of recaptured fish to use the method of Brownie et al. (1985) to estimate annual survival.

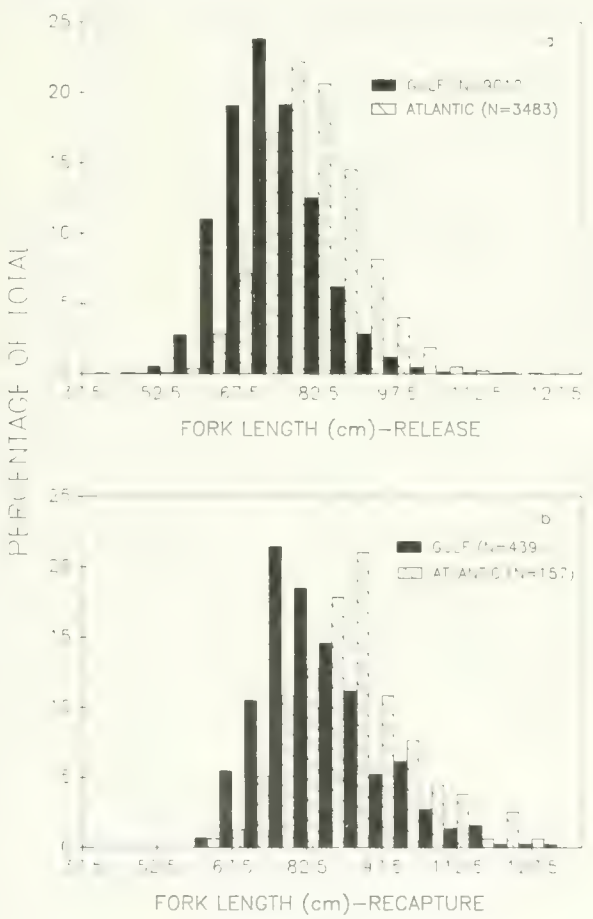

Figure 1

Length-frequencies of king mackerel *Scomberomorus cavalla* at release and recapture from Gulf of Mexico and Atlantic migratory groups. Fish were grouped by 50 mm FL intervals; mid-range values are used for each plot.

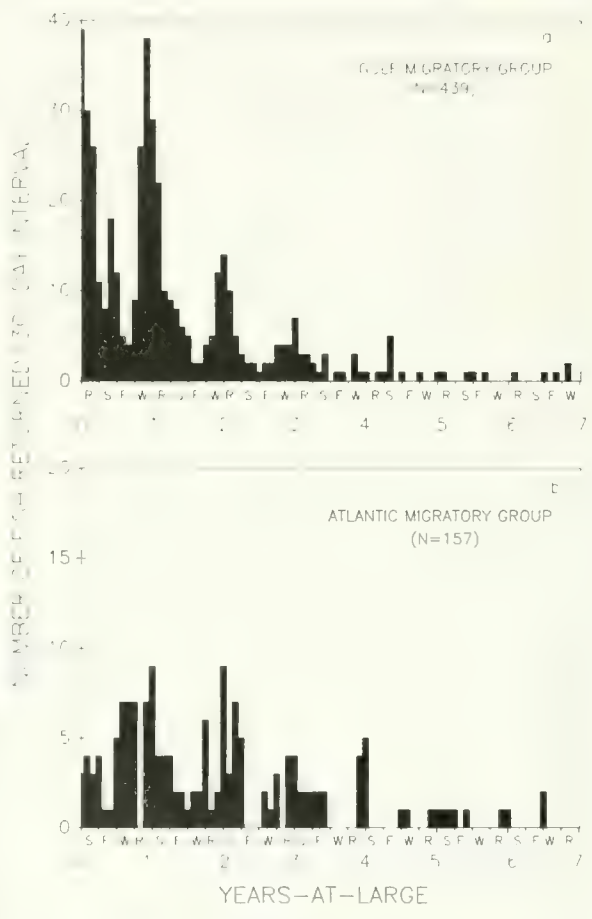

Figure 2

Recaptured king mackerel *Scomberomorus cavalla* utilized in the growth analysis, summarized by 30-day blocks from time of tagging, for the Gulf of Mexico (released during December–March) and Atlantic (released during May–June) migratory groups. Seasons for each year of recapture are: W = winter, R = spring, S = summer, and F = fall.

Table 3

Summary of theoretical growth parameters (L_∞, K) and mortality estimates (Z), sexes combined, for Gulf of Mexico and Atlantic migratory groups of king mackerel *Scomberomorus cavalla*.

Study	Migratory group	Interval	L_∞ (cm)	K	Z
Present study	Gulf of Mexico	1975–88[1]	132.6	0.127	0.794 (1976–82[2]) 0.877 (1977–82[2]) 0.766 (1978–84[2])
	Atlantic	1975–85[1]	152.0	0.070	0.658 (1976–82[2]) 0.493 (1977–82[2]) 0.582 (1979–84[2])
Manooch et al. (1984)	Gulf of Mexico	1980–85	147.8	0.115	0.54 (1980[3]) 0.72 (1981[4]) 0.50 (1984[5])
Collins et al. (1988)	Atlantic	1983–87	112.7[6] 127.7[7]	0.213[6] 0.087[7]	Not available

[1]Time from release to recapture used in calculating growth parameters.
[2]Years used in regression analysis of recaptured king mackerel.
[3]Year fish collected from recreational hook-and-line catches in northwest Florida.
[4]Year fish collected from gillnet catches in south Florida.
[5]Year fish collected from south Florida purse-seine catches.
[6]Whole otoliths.
[7]Sectioned otoliths.

Results and discussion

Growth analysis

A total of 9010 king mackerel from the Gulf of Mexico king mackerel migratory group were tagged; 794 were reported recaptured, and 439 fulfilled our criteria for inclusion in the growth analysis. The mean length-at-tagging was 74.5 cm FL (SD 8.92 cm, range 42.5–120.0 cm) (Fig. 1a), while the mean length-at-return was 85.2 cm FL (SD 11.61 cm, range 62.5–133.0 cm) (Fig. 1b). Maximum time-at-large was 10.48 years (3829 days), with a mean of 1.06 years (SD 1.24 yr). Fish were recaptured most frequently during the first year of freedom (51.5%), with seasonal increases in returns noted during winter and spring months (Fig. 2a). We recaptured Gulf of Mexico migratory group fish from Texas to southeast Florida through 1988, although 95.5% were taken before 1981.

The relationship between length-at-return minus length-at-tagging ($\Delta\ell$) vs. number of days-at-large (Δt) for Gulf of Mexico king mackerel was described by: $\Delta\ell = 3.722 + 0.012\ (\Delta t)$ (r^2 0.503; df 1, 438; $P<0.01$). Mean values from a total of 63 30-day blocks were used to generate an estimate of $L_\infty = 132.6$ cm FL (95% CI 114.3–150.8 cm), and K = 0.127 (95% CI 0.068–0.186). Manooch et al. (1987) used whole otoliths to calculate an L_∞ value of 147.8 cm (95% CI 131.6–164.0 cm) and K = 0.115 (95% CI 0.079–0.152) for Gulf of Mexico king mackerel captured during 1980–85 (the majority taken from Key West, northwest Florida, and Texas), combining both sexes (Table 3). Growth parameters determined from our tagging study overlap the spatial and temporal constraints of their age-length data.

A total of 3483 king mackerel were tagged from the Atlantic king mackerel migratory group. Recaptures were reported for 253 fish, of which 157 provided sufficient data for our growth analysis (Fig. 1b). Mean length-at-tagging was 81.0 cm FL (SD 9.17, range 50.0–122.5 cm), while the mean length-at-return was 91.0 cm FL (SD 11.65, range 64.8–127.0). The maximum time-at-large was 6.47 years (2361 days), with a mean of 1.56 years (SD 1.41 yr). Fewer returns were reported during the first year of freedom (31.2%) than were noted for the Gulf migratory group (Fig. 2b), and most returns occurred during the summer and fall. We recaptured Atlantic migratory-group king mackerel through 1985; however, 92.1% were taken before 1982, prior to commercial and recreational quota restrictions.

The relationship between growth ($\Delta\ell$) and time-at-large (Δt) for the Atlantic fish is: $\Delta\ell = 4.057 + 0.008\ (\Delta t)$ (r^2 0.323; df 1, 156; $P<0.01$). The estimated asymptotic length for Atlantic king mackerel calculated from 52 30-day blocks was 152.0 cm FL (95% CI 87.3–216.8 cm), with an associated K = 0.070 (95% CI 0.005–0.146). Collins et al. (1988) used whole and sectioned otoliths from king mackerel in the Atlantic group to calculate estimates of $L_\infty = 112.7$ and 127.7 cm FL, and K = 0.213

and 0.087 (whole vs. sectioned, respectively) for fish collected from Cape Canaveral, Florida, to Cape Fear, North Carolina, during 1983–87 (Table 2). They concluded, however, that whole otoliths may have provided biased estimates, at least for Atlantic king mackerel. Although the spatial distribution of our tagging effort was similar to the geographical study area of Collins et al. (1988), their collections occurred during regulation of the king mackerel fishery.

Comparison of our growth estimates for Gulf and Atlantic king mackerel should be made with caution due to our limited sample size and our reliance on reported fish lengths. The Atlantic group appears to exhibit a larger maximum size (L_∞) and a slower relative growth rate (K) than its Gulf of Mexico group counterparts (Table 2). This is supported by comparing the two regression equations of growth ($\Delta\ell$) vs. time-at-large (Δt). We found that the slope for the Gulf of Mexico group was significantly different (ANCOVA; F 7.344, df 1, 592; $P<0.01$) than that observed for the Atlantic king mackerel, indicating a faster growth rate over the size range that were tagged and recaptured.

Growth analyses using age-length data provide an estimate of asymptotic mean length-at-age, while mark-recapture data provide estimates of the maximum length achieved in the population (Francis 1988). Our L_∞ estimate for the Gulf of Mexico migratory group (132.6 cm) was larger than that for any individual fish tagged or returned, except for one fish which was 133.0 cm FL; however, Trent et al. (1987) found fish as large as 158.0 cm FL in their work off Louisiana. These large fish were females taken from what may be a year-round resident population (Fable et al. 1987) which was not included in our tagging efforts. Fish from the Gulf of Mexico migratory group that were tagged in our study would therefore be considered part of the 'small' migratory fish described by Fable et al. (1987). Manooch et al. (1987) reported sampling fish up to 180.2 cm FL from the Gulf of Mexico; however, because they did not provide a length distribution, the frequency of fish larger than 132.6 cm FL in their samples could not be determined. All fish collected from both the Collins et al. (1988) and our study were smaller than the calculated L_∞ values for the Atlantic migratory group.

Annual survival rates

Between 1976 and 1984, estimates of survival rates were lower for the Gulf migratory group than those observed for the Atlantic migratory group of king mackerel (Table 3). Regression and maximum-likelihood techniques yielded similar estimates of survival rates for the Gulf group. Annual pooled estimates of survival rates of these fish were in the range 41.6–46.5% (Z 0.877–0.766/yr; Table 3). The simplest model of Brownie et al. (1985; Model 3, constant survival and recovery rates, independent of age) was the most applicable to our database for the Gulf group of king mackerel, yielding a pooled estimate of 42.290 (SE 1.60; Z 0.794/yr). Estimates of annual survival rates for the Atlantic migratory group were in the range 51.8–61.1% (Z 0.658–0.493/yr).

Previous estimates of annual survival rates generated from age-length data compare favorably with those calculated from our mark-recapture data. Manooch et al. (1987) calculated instantaneous total mortality estimates from age-length data for king mackerel from two locations in the Gulf of Mexico that overlapped with our study area (Table 3). Their estimates of annual survival rates were in the range 48.7–60.7% (Z 0.719–0.499/yr) for king mackerel (both sexes combined) in south Florida collected during 1981 (gillnet) and 1984 (purse seine). King mackerel collected from recreational hook-and-line catches in northwest Florida during 1980 yielded an annual survival rate estimate of 58.3% (combining sexes; Z 0.540/yr). A pooled estimate of annual survival rate for king mackerel collected during 1977–79 along both the Gulf and Atlantic coasts was 63.0% (Z 0.462/yr; Johnson et al. 1983).

Growth and mortality estimates generated from age-length and length-increment studies must account for behavioral characteristics germane to a migratory species. King mackerel have been shown to have at least two migratory patterns along the southeastern United States; however, there is a seasonal overlap of the two groups along southeast Florida that may be as high as 29.4–41.8% (Sutter et al. 1991). Resident populations of king mackerel may also exist in the northcentral Gulf of Mexico (Fable et al. 1987) and in southeast Florida waters (Sutter et al. 1991). These factors should be considered when designing future survey strategies to describe growth and mortality rates.

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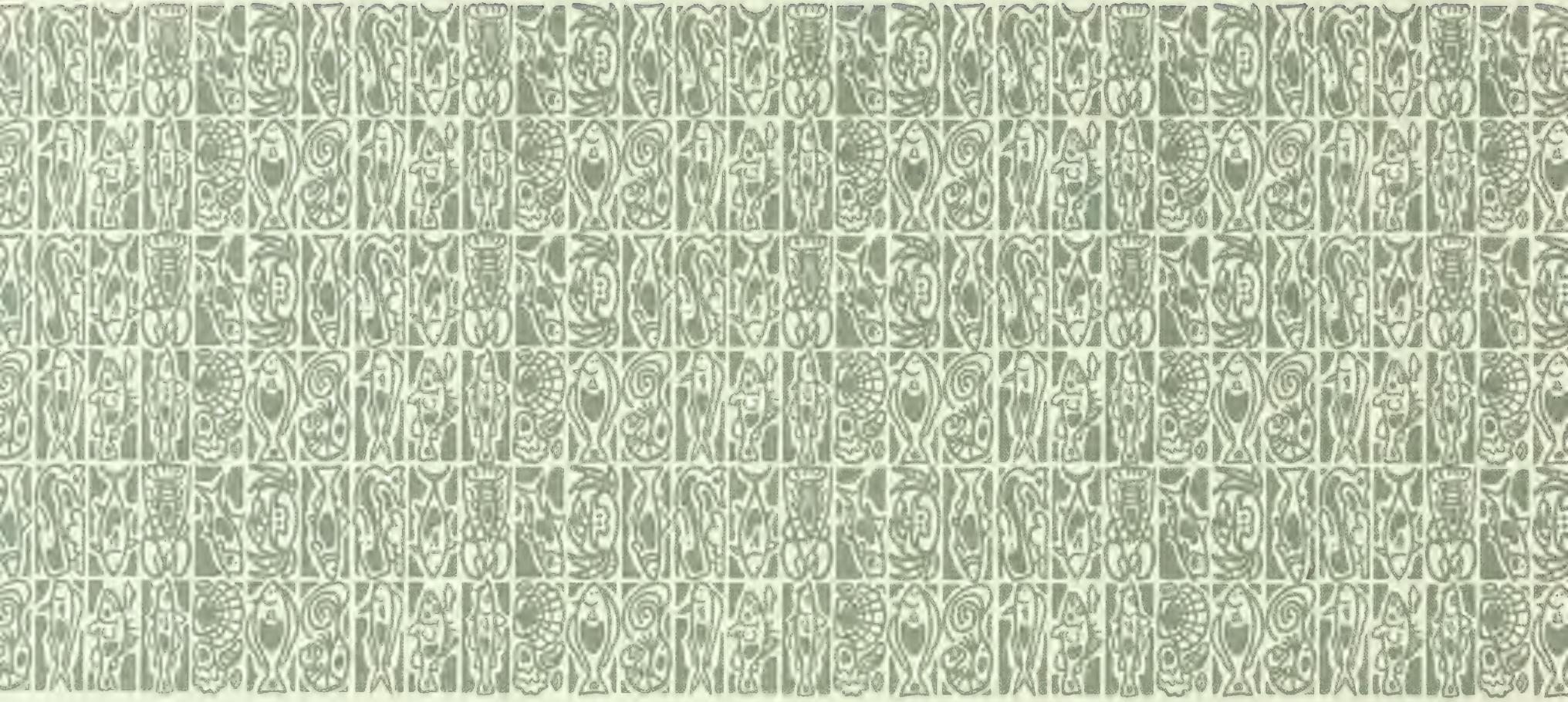

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